Crop Pollination by Bees

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Preface

Pollination is the most important contribution bees make to human economies. The value of honey and beeswax pales in comparison to the value of fruits, vegetables, seeds, oils, and fibres whose yields are optimized by pollinating bees. There was a time when it was relatively easy to overlook this benefit, and it may be possible still in particular areas and cropping systems in which there are large and sustainable populations of bees, whether managed or naturally occurring. In such places the rich background of pollinators means that pollination rarely is a limiting factor in crop production. Many parts of North America fit this description prior to the 1980s. But the cropping systems and pollinator demographics in many countries are changing profoundly, and a let-alone approach to pollination will prove increasingly inadequate for meeting the demands for an abundant, high-quality food supply into the 21st century.

It is becoming manifestly clear that our bee pollinators are a valuable and limited natural resource that should be conserved and encouraged at all costs. This awareness stems in part from an apparent decline of the western honey bee, *Apis mellifera*, that is occurring in many parts of the world. The decline of honey bees stems from more than one cause, but the most straightforward explanation is the rapid spread of parasitic varroa mites that occurred worldwide in the closing decades of the 20th century. Varroa is relatively innocuous on its natural host, the eastern honey bee, *Apis cerana*, but on *A. mellifera* it is devastating. The parasite occurs now on every continent on which *A. mellifera* is kept, except Australia, and it is considered the most serious health threat to apiculture (Matheson, 1993, 1995). The perception of a pollination crisis proceeds also from a general increase in the area of bee-pollinated crops. In some countries the demand for pollination is increasing at the very time that the supply of managed pollinators is decreasing.

The so-called pollination crisis has generated a renewed interest in the management, culture, and conservation of pollinating bees. We

believe that it also creates the need for an updated book on applied bee management and conservation for crop pollination.

We are heavily indebted to two authoritative texts, S.E. McGregor's 1976 *Insect Pollination of Cultivated Crop Plants* and J.B. Free's 1993 *Insect Pollination of Crops*, 2nd edition. These texts virtually define the state of the science of crop pollination and remain the first stop for academicians looking for comprehensive research reviews. With this book our goal was not to duplicate another comprehensive review, but rather to synthesize the latest scientific literature into principles and practices that are relevant to workers in crop pollination. This book is primarily for agricultural consultants, extension specialists, plant and bee conservationists, crop growers, bee-keepers, and others with an interest in applied pollination.

We concentrate on bee-pollinated crops of significant or emerging economic importance in the temperate developed world, crops for which there is a strong bee pollination story in the literature, and crops for which pollination is historically a limiting factor. Pollination is a multifaceted component of crop production and not easily reduced to formula recommendations. Nevertheless, some practical recommendations should come out of a book like this if we hope to help crop growers and bee-keepers. One example is a recommended density of bees. This information is difficult to synthesize because the literature is often scarce or incongruent. It is scarce because it is difficult and expensive to experimentally control large acreages for rigorous scientific studies or to separate out the contribution of any one bee species. It is incongruent because results vary among different regions and researchers do not always test the same hypotheses or measure the same parameters. Rather than weary readers with a review of this difficult literature, we present research and extension service recommendations in table format for most crops and give a literature average for recommended bee densities. Although other considerations must enter the decision-making process, this approach gives growers and bee-keepers a rational starting point.

In much of the developed world, the last 30 years have seen changes in the bee-keeping industry that approach in magnitude the technological revolutions of the 19th century. Chemical controls aimed at parasitic varroa mites have transformed the industry from one that was relatively pesticide free to one that is now virtually pesticide dependent. In the Americas, the Africanized honey bees, a highly defensive race of bee introduced to Brazil from Africa in the 1950s, spread through tropical and subtropical regions, altering bee-keeping practices, raising liability risks, disrupting crop pollination, and competing with native pollinators. Faced with problems like these, many bee-keepers have gone out of business, leaving behind a pollination vacuum.

One result is a renewed interest in non-honey bees, some of which are very good pollinators. Called non-managed bees, pollen bees, wild bees, or non-*Apis* bees, these are solitary or social bees that nest primarily in simple burrows in grass thatch, wood, plant stems, or soil. Methods for mass rearing most of them are impractical, and their management often translates to conserving and enhancing wild populations. Bee conservation is not a mature science. In Europe it is in its adolescence. In North America it is embryonic. But in this book we highlight the emerging principles and, where justified, give recommendations for enhancing populations of non-honey bees. This requires some discussion of bee ecology and conservation biology, but here again our goal is to make the science relevant in the context of crop pollination.

Finally, in this book we hope to engender an appreciation for *all* bee pollinators – managed or non-managed, exotic or native – and an honest recognition of the assets and limitations of each. The western honey bee is an exotic species in much of its modern range. It is rarely the most efficient pollinator, but it is very manageable. Conversely, some native specialist bees are extremely efficient pollinators but their numbers can be low and unpredictable. It is counterproductive to debate the comparative strengths and weaknesses of different bee pollinators or, even worse, to advocate only one pollinator or group of pollinators. The truth is, we need all the pollinators we can get. And that is the goal of this book – to promote a large, diverse, sustainable, and dependable bee pollinator workforce that can meet the challenge for optimizing food production well into the 21st century.

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Chapter 1

Benefits of Bee Pollination

This book is for anyone interested in using bee pollination to improve yield and quality of cultured plant products. For many important crops, good bee pollination translates into higher yield, larger fruit, higher quality fruit, and faster ripening fruit. These benefits translate not only into optimized incomes for growers, but ultimately into a large and diverse food supply that promotes human health and well-being. It is no exaggeration that the sheer abundance, high quality, and variety of food enjoyed today in much of the developed world – a bounty unmatched by any other period in history – derives in no small measure from bee pollination.

The western honey bee (*Apis mellifera* L.) is arguably the most well-known bee pollinator of crops. Its native range is large, extending from northern Europe, through the Middle East, and all of verdant Africa. Beginning in the 17th century, European colonists began actively spreading this bee throughout much of the world. In the ensuing centuries *A. mellifera* has proven itself highly adaptable to a broad range of climatic conditions. Its adaptability, its tolerance of human management, and its honey-making habit have secured its place as humanity's favourite bee. Large feral populations of honey bees became the norm in much of the world, populations that contributed significantly to crop pollination, with or without the knowledge or appreciation of the farmer. Today, many countries have large and sophisticated bee-keeping industries dedicated to the production of honey, other hive products, and pollination services.

Bee-keeping is a viable agricultural pursuit in developing countries, but the bee-keeping industries in many developed countries have contracted. World honey prices have been depressed the last few decades owing in part to the availability of other cheaper sweeteners. Parasitic varroa mites (*Varroa* sp.) and tracheal mites (*Acarapis woodi*) have spread from their native ranges and killed untold thousands of managed honey bee colonies and virtually eliminated feral populations in places.

One result of these hardships has been a renewed interest in the use of bumble bees and solitary bees as commercial pollinators. Only a few species of such alternative pollinators have been successfully cultured, so there is an emphasis on conserving their natural populations. There is great need for research in the conservation, culture, and use of these bees for pollination. Naturally-occurring bee populations are not always dependable for commercial pollination needs, owing to their uneven distribution or loss of their natural habitats and food plants. Rearing and managing methods for some non-honey bees are finely worked out and practical, but for others the rearing methods are poorly developed or protected as proprietary secrets.

One of our aims in this book is to promote an appreciation of all available bee pollinators. Pollinating bees, whether managed or naturally-occurring, are a valuable and limited resource. In this book, we concentrate on managing and conserving bees to optimize crop pollination. We cover honey bees, other managed bee species, and wild non-managed species. Each group has assets and liabilities from a plant grower's point of view, but each deserves our best efforts to maintain its populations through good management or conservation.

Bee Pollination in Perspective

Since good pollination increases fruit yield and quality, farmers have long been interested in this phenomenon. The civilizations of the ancient Middle East understood, at least in a practical sense, the importance of pollination. A bas relief from Assyria dating around 1500 BC shows mythological creatures manually cross-pollinating date palms (Real, 1983). The prophet Amos in the 8th century BC was a 'piercer of sycamores', a practice still done today in which poorly-pollinated figs are manually gashed to induce ripening (Dafni, 1992).

Today, 90% of worldwide national per capita food supplies are contributed by 82 commodities that can be assigned to plant species and by 28 general commodities (such as hydrogenated oils) that cannot be assigned to particular species. Bees are pollinators for 63 (77%) of the 82 species commodities, and they are the most important known pollinator for at least 39 (48%) (Prescott-Allen and Prescott-Allen, 1990; Buchmann and Nabhan, 1996). The multiplicative value of bee pollination becomes apparent when one tallies bee-pollinated food plants and considers the large quantities that are converted to animal feeds and ultimately meat, egg, and dairy products. One well-worn, and probably accurate, estimate says that one-third of the human diet can be traced directly, or indirectly, to bee pollination (McGregor, 1976). This estimate is probably more accurate for human diets in developed countries.

Although wind-pollinated cereals make up the bulk of human diets (Thurston, 1969), insect-pollinated crops often mean the difference between eating for survival or eating for pleasure. Insect-pollinated crops are the delicacies one can easily take for granted. They are the low-acreage, high-value crops that pump millions of dollars into local agricultural economies. They are the forage plants that fuel livestock production. To gain an appreciation of bee pollination, one need only imagine life without beef steak, blueberry muffins, ice cream, pickles, apple dumplings, or watermelon. For many people in the world, such deprivations are not imaginary. If the gross disparities that exist in the world between rich and desperately poor, well-fed and not, are ever to be absolved, bee pollination will play a part.

The area of bee-pollinated crops is increasing in many developed countries (Torchio, 1990a; Corbet *et al.*, 1991). In Canada, over 17% of cultivated land is used for crops that depend entirely or in part on insect pollination (Richards, 1993). If developing countries follow suit, we can expect unprecedented growing demand for bee pollination in the 21st century.

Benefits of Bee Pollination

About 130 agricultural plants in the USA are pollinated by bees (McGregor, 1976), and the annual value of honey bee pollination to US agriculture has been estimated at over US$9 billion (Robinson *et al.*, 1989). A later study took into account the benefits of non-managed bees and more conservatively placed the value of honey bees between US$1.6 and $5.7 billion (Southwick and Southwick, 1992).

The annual benefit of honey bee pollination in Canada is estimated at Can$443 million, and over 47,000 colony rentals take place every year. Every dollar spent on colony rental fees in Québec returns Can$41 for blueberries and Can$192 for apples (Scott-Dupree *et al.*, 1995).

In the UK there are at least 39 crops, grown for fruit or seed, that are insect pollinated. Honey bees and bumble bees make up the majority of insect visitors to these crops. In an analysis of 13 of the major field crops and two glasshouse crops, it was estimated that the annual value of insect pollination in the UK is £202 million. The portion of that amount attributable to honey bee activity on field crops is estimated at £137.8 million (Carreck and Williams, 1998).

Borneck and Bricout (1984) and Borneck and Merle (1989), working with the 30 most important insect-visited crops in the European Union (EU), determined that insect pollination has an annual estimated value of €5 billion, with €4.3 billion of that attributable to honey bees.

The degree to which a particular crop needs insect pollination depends on the flower morphology, level of self-fertility exhibited by the plant, and arrangement of flowers on the plant or on neighbouring plants. Those crops are most dependent on insect pollination that have separate male and female flowers (so-called imperfect flowers), whether occurring on separate plants or on the same plant. In these cases insects, especially bees, are important pollen vectors, moving pollen from male to female flowers. There is a higher rate of self-pollination in plants with flowers housing both male and female sexual components (perfect flowers); however, bees often optimize pollination even in perfect flowers. Pollination in other crops, particularly the cereals, is accomplished by wind and gravity, and bees play only a minor role.

It is thus possible to categorize crops according to their degree of dependence on bee pollination, and it follows that the economic value of bee pollination is highest in those crops most dependent on bee pollination. In Table 1.1 we list some published insect-dependence categories for most of the crops addressed in this book.

So far we have been discussing the economic benefits of bee and insect pollination at national or continental levels. But to be implemented nationally the benefits of bee pollination must be realized locally by individual growers and bee-keepers. The best documentation of potential grower benefit from bee pollination is a series of papers from Washington and British Columbia in western North America. The researchers were primarily interested in the demonstrated efficacy of a novel synthetic bee attractant, but their design provided a convenient way to compare local yields under different pollination regimes. By optimizing honey bee pollination with the synthetic bee attractant, the researchers caused:

- increased fruit size in pears which translated to a US$162–427 acre^{-1} (US$400–$1055 ha^{-1}) increase in farmgate revenue;
- a 41% increase in cranberry yield with a US$3564 acre^{-1} (US$8804 ha^{-1}) increase in revenue; and
- a 7% increase in blueberry yield with a US$399 acre^{-1} (US$986 ha^{-1}) increase in revenue (Currie *et al.*, 1992a,b; Naumann *et al.*, 1994b).

The rental of honey bee colonies for commercial pollination is a viable component of the bee-keeping industries in some developed countries. The importance of pollination to a regional bee-keeping industry has been documented in a regular annual survey in the northwest US (Burgett, 1997, 1999). Commercial bee-keepers in this region received over 60% of their annual gross revenues from colony rentals in 1998 and 72% in 1995. Demand exceeded supply during much of the 1990s and this led to favourable market conditions for

Table 1.1. Degree of dependence of selected crops on insect pollination. Values are 0.1–1.0 in scale of increasing crop dependence on bees or other insects. Values for Robinson *et al.* (1989) are the projected fraction of crop lost in the USA in the event there were no honey bees. The worst-case loss estimate of Southwick and Southwick (1992) assumes a total loss of honey bees and no changes in current management practices for non-honey bees in the US. The expected loss estimate of Southwick and Southwick assumes 50% loss of honey bees in northern US states due to parasites and disease, 100% loss of European honey bees in southern states due to expansion of Africanized bees, and some increase in the use of non-honey bees. The fifth column gives the insect-dependence values presented by Williams (1994) for the EU; values in this column must be interpreted with caution in the present context because they were derived from numerous published reports, including that of Robinson *et al.* (1989).

Crop	Robinson *et al.* (1989)	(Southwick and Southwick, 1992) Worst-case	(Southwick and Southwick, 1992) Expected	Williams (1994)
Alfalfa (Lucerne) seed	0.6	0.7	0.2	1.0
Almond	1.0	0.9	0.5	1.0
Apple	0.9	0.8	0.3	1.0
Asparagus seed	0.9	0.9	0.1	1.0
Avocado	0.9	0.2	0.1	1.0
Bean (lima)	NA	NA	NA	0
Bean (common)	NA	0.1	0.03	0
Beet seed	NA	0.1	0	0.1
Blueberry	NA	NA	NA	Great
Cabbage seed	NA	0.9	0.5	1.0
Canola	NA	NA	NA	Moderate
Cantaloupe	0.7	0.7	0.5	0.8
Carrot seed	0.9	0.6	0.1	1.0
Cherry	0.8	0.6	0.3	0.9
Clover (alsike)	NA	NA	NA	Essential
Clover (crimson)	NA	0.5	0.3	Great
Clover (red)	NA	0.25	0.12	Essential
Clover (white)	NA	0.2	0.1	Essential
Clover (sweet)	NA	0.1	0.05	NA
Cotton seed	0.2	0.3	0.2	0.2
Cranberry	0.8	0.4	0.3	1.0
Cucumber	0.8	0.6	0.3	0.9
Kiwifruit	NA	NA	NA	0.9
Onion seed	0.9	0.3	0.2	1.0
Peach	0.5	0.2	0.1	0.6
Pear	0.6	0.5	0.3	0.7
Plum and prune	0.6	0.5	0.3	0.7
Raspberry	NA	NA	NA	Moderate
Soybean	0.1	0.01	0	Moderate
Squash	NA	NA	NA	0.9
Strawberry	NA	0.3	0.2	0.4
Sunflower	0.9	0.8	0.5	1.0
Tomato	NA	NA	NA	Moderate
Watermelon	0.6	0.4	0.1	0.7

NA, not available.

bee-keepers. The average rental price per colony received by bee-keepers increased from US$19.25 in 1992 to US$31.55 in 1996. During the same period, the average annual revenue from colony rentals increased a remarkable 246% from US$37,993 in 1992 to US$131,625 in 1996.

For fruit- or nut-bearing crops, pollination can be thought of as a grower's last chance to increase yield. It is the degree and extent of pollination that dictates the maximum possible number of fruits. All post-pollination inputs, whether growth regulators, herbicides, fungicides, or insecticides, are generally designed not to increase yield but to conserve losses. Because of its yield-optimizing benefits, bee pollination can play an important role in maintaining a sustainable and profitable agriculture with minimized disruptions to the environment. Alterations in agricultural practices that significantly reduce yield rates have the danger of encouraging more wild lands to be converted into farmland to make up for reduced yields (Knutson *et al.*, 1990). Good bee pollination and optimized crop yields are thus part of a sound environmental management policy.

Finally, the economic value of bee pollination goes beyond production agriculture because bees pollinate more than just crop plants. All told, bees pollinate over 16% of the flowering plant species in the world (Buchmann and Nabhan, 1996). Bee pollination sustains native and introduced plants that control erosion, beautify human environments, and increase property values. Bees pollinate native plants which provide food for wildlife and have inherent value as members of local natural ecosystems. Although some believe that this generalization does not apply to the cosmopolitan honey bee, *A. mellifera*, which is an exotic species throughout most of its modern range, the bulk of experimental evidence suggests that introduced honey bees are only rarely a detrimental feature of local ecologies (Butz Huryn, 1997). In the absence of large-scale demonstrable negative impacts of introduced honey bees and considering their widely acknowledged value as pollinators of crop plants and their catholic plant preferences, it seems reasonable to anticipate that honey bees, even introduced populations, play an important role in sustaining natural plants and the animal communities that depend on them (see Chapter 3, page 22).

Efforts to quantify the value of bee pollination to human societies face daunting obstacles. As we have seen, the arguments must be not only economic or ecological, but, we propose, philosophical. It is possible to make reasonably accurate estimates of the economic value of bee pollination in food and fibre production, thanks to institutionalized record keeping in the agricultural sector. But one senses that this is only the tip of the iceberg. Insofar as bee-dependent plants touch human life, whether providing us with a bountiful food supply or a

pleasant walk through City Park, humans are dependent on bees. Bees may not be necessary to human life, but they are necessary for life as we know it.

Chapter 2

Bee Pollination

Pollination is the transfer of pollen from the male parts (*anthers*) of a flower to the female part (*stigma*) of the same or different flower. If the pollen is compatible, fertilization of the ovule and seed formation can occur. More seeds develop when large numbers of pollen grains are transferred. Seeds, in turn, stimulate surrounding ovary tissue to develop so that, for example, an apple with many seeds will be larger than one with fewer seeds. In this way, good pollination improves both fruit yield and size. Pollen may be transferred by wind, gravity, water, birds, bats, or insects, depending on the plant. Some flowering trees in the tropics are pollinated by monkeys (Gautier-Hion and Maisels, 1994), and in Japan at least one company grows and markets a fly that pollinates strawberries and other crops (Matsuka and Sakai, 1989). Worldwide, bees are the most important pollinators owing to their vegetarian diet, flower-visiting habit, and hairy bodies that readily pick up pollen grains (see Chapter 3).

The Flower and the Fruit

A *flower* is a plant organ designed for sexual reproduction. An *inflorescence* is an arrangement of flowers on a stem. There are several types of inflorescences – single flower, head, raceme, panicle, spike, and umbel (Fig. 2.1). The main stem of an inflorescence is the *peduncle*, and the stem of any individual flower is the *pedicel*.

The outer whorl of petals is called the *corolla* (plural *corollae*) and is designed to protect the interior sexual parts, to exclude ineffective pollinators, to attract effective pollinators, and to direct effective pollinators towards the inside of the flower. In legume-type flowers, two anterior petals join to form a *keel* inside which are housed the sexual parts of the flower. Male parts of a flower are called the *stamens*, each made up of a slender *filament* holding an *anther* at the tip. When it is

Fig. 2.1. Some examples of inflorescence designs. (Source: Darrell Rainey.)

mature, the *anther* opens and releases *pollen grains* which contain the equivalent of animal sperm. Female parts of a flower are called the *pistil*, each made up of an *ovary* with *ovules* and a stalk-like *style* with a sticky *stigma* on top (Fig. 2.2).

A flower with both stamens and pistil is called a *perfect* flower. Many plants have flowers that are *imperfect*, that is, only male or only female. Sometimes both types of imperfect flowers occur on the same plant. It is easy to identify imperfect female flowers in cucurbit crops (cantaloupe, cucumber, gourd, pumpkin, squash, watermelon) because of the large ovary at the flower's base which later develops into a mature fruit.

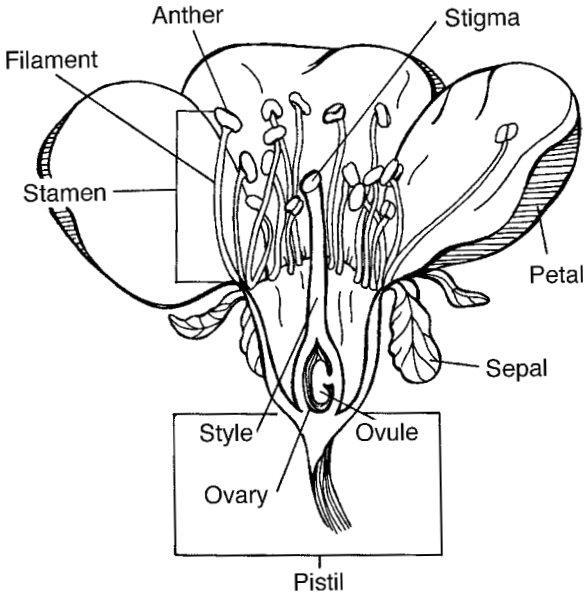


Fig. 2.2. General morphology of a perfect flower. (Source: Carol Ness.)

When a pollen grain lands on a receptive stigma, it grows a *pollen tube* down the style to the ovary. Male genetic material passes down the pollen tube and fertilizes an ovule. Ovules become seeds and the surrounding ovary develops into the fruit. This process is called *fruit-set*.

A single pollination episode does not necessarily guarantee fruit-set. Pollen in sufficient quantities must reach the stigma while its surface is receptive, the pollen must be compatible, and pollen tubes must successfully grow down to and penetrate the ovules. Many things can go wrong. Transfer of pollen can be poor if the pollinator population is low or bad weather keeps pollinators from foraging. Female flowers are often most receptive to pollen in early morning, and anything that disturbs morning bee visitation, such as rain, can impair pollination even if bees are active for the rest of the day. An absence of compatible blooming *pollenizers* (sources of pollen) can prevent good pollination in plants that require inter-varietal cross-pollination such as apples and rabbiteye blueberries.

Flower structures vary widely, and there are many types of fruit. A *berry*, such as tomato, has a fleshy outer wall surrounding one or more fairly small seeds. A *pome*, such as apple, has a fleshy outer wall surrounding a tough core with seeds. A *drupe* or *stone* fruit,

such as peach, has a fleshy outer wall surrounding one stony seed. With *aggregate* fruits, such as strawberry and raspberry, many pistils develop together as a single mass. If pollination is poor in ovaries with more than one ovule (such as berries and pomes) or in multiple neighbouring ovaries (such as aggregate fruits), ovarian tissue develops only around those ovules that are fertilized. This is a cause of misshapen fruit in many crops.

Plant Pollination Requirements and Definitions

Not all flowering plants have the same pollination requirements.

Cross-pollination is the transfer of pollen from flowers of one plant to the flowers of a different plant or different variety. Many crops require or benefit from cross-pollination.

Self-fertile plants can develop seeds and fruit when pollen is transferred from anthers of a flower to the stigma of the same flower or different flower on the same plant. However, such plants are not necessarily *self-pollinating*. Insects still may be necessary or helpful in moving pollen to the stigmas. Interplanting of varieties is not necessary but may be helpful; for example, many self-fertile crops, such as Swede rape (canola) and highbush blueberry respond well to cross-pollination.

Self-sterile plants require pollen from a different plant or even a different variety. If the plant requires different varieties, the grower must interplant pollenizer varieties with the *main* variety. *Cross-compatible* varieties are receptive to each other's pollen, whereas *cross-incompatible* varieties are not. Seed and nursery stock catalogues usually provide tables that cross-list compatible varieties.

Monoecious plants have both male and female flowers on the same plant. *Dioecious* plants have only one sex of flower on the same plant, rendering cross-pollination obligatory.

Parthenocarpic plants develop fruit without requiring the pollination process, and that being the case, parthenocarpic fruits can be partially or completely seedless. There are plant growth regulators that can be applied to induce plants, even plants normally cross-pollinated, to develop fruit parthenocarpically. This is the case in rabbiteye blueberry with the growth regulator gibberellic acid which is applied in early spring to augment natural pollination. It is important to treat these chemicals as supplements for pollination, not its replacement. Support for this assertion was found in Florida where blueberry fruit weight was maximized when gibberellic acid was used in conjunction with saturation (hand) pollination (Cano-Medrano and Darnell, 1998).

Bees and Pollination

Many insects visit flowers to collect pollen as food. As they do this they pollinate the flowers. Most flowers offer sugary liquid *nectar* as a reward for these pollinating insects. Bees are especially effective insect pollinators because they eat pollen and nectar almost exclusively, visit many flowers of the same species during a single trip, and have hairy bodies that easily pick up pollen grains. There is a close association between flowering plants and bees. Bees pollinate over 16% of the world's flowering plant species (Buchmann and Nabhan, 1996) and nearly 400 of its agricultural plants (Crane and Walker, 1984).

Ecology of Bee Pollination

Although bees and bee-pollinated flowering plants depend on each other, both operate selfishly. For each, there is a cost/benefit equation that must balance in its favour. Nectar and pollen production are costly to a plant and must be balanced for maximum return (that is, maximum chance of successful reproduction) for the energy spent to produce them. For example, individual flowers must contain enough nectar to attract pollinators, but little enough to keep pollinators motivated to visit many flowers, thus accomplishing pollination. Some plants accomplish this strategy by putting heavy nectar loads in only a few (5–8%) of their flowers. These constitute the so-called 'lucky hits' for a bee (Southwick *et al.*, 1981) that motivate it to keep foraging on the plant. Flight and foraging activity are energetically costly to a bee and must be balanced against the calories derived from nectar and pollen.

A large body of ecologic literature, called *optimal foraging theory*, predicts that foraging animals will forage efficiently, moving between food patches and lingering in food patches in such a way as to get the most return for their effort. When such hypotheses are tested in the field, they have often proved true. It is beyond the objectives of this book to treat this rich topic exhaustively, but we have selected for discussion a few principles of bee ecology that have implications for commercial crop pollination management.

Bee foraging distances from nest

It has been shown that honey bees are capable of flying several miles to forage if necessary, but they forage preferentially near their nest if the resource richness permits (Gary and Witherell, 1977). This implies

that honey bee colonies used for crop pollination should be placed relatively near the target crop. Interestingly, the matter is reversed for bumble bees which prefer to forage on resources 164–2070 ft (50–631 m) from their nest (Dramstad, 1996; Osborne *et al.*, 1999). However, this fact has little bearing on commercial bumble bee pollination because bumble bees are most often used in glasshouses in which their foraging range is artificially limited.

Bee foraging activity at rich or poor resources

From a pollination perspective, bee foraging activity is generally more efficient in flower patches that are rich in nectar and pollen. It has been shown that animals forced to forage in resource-poor habitats tend to spend more time at each food site than do animals in rich habitats (Pyke *et al.*, 1977). It is advantageous for insects to be moving rapidly between flowers, accomplishing a high rate of pollination, rather than lingering for relatively long periods on the few flowers in a patch that are yielding nectar. Southwick *et al.* (1981) demonstrated that bee visitation rates increased in flower patches with increasing number of nectar-bearing flowers, nectar volume, and sugar concentration of nectar.

Not only do resource-rich plantings encourage rapid bee visitation between flowers, but they encourage pollinators to stay in that patch. It was shown that bumble bees and honey bees that have just visited highly-rewarding flowers fly shorter distances before visiting another flower than do bees that have just visited less rewarding flowers (Pyke, 1978; Waddington, 1980). This behaviour increases the likelihood of the bee encountering another rewarding flower in a site which is shown to be profitable.

Collectively, these studies make a strong argument for improving the nectar and pollen production output of our important bee-pollinated crops. Optimal foraging theory predicts that if nectar output of a crop is relatively high, bees pollinate more efficiently because they visit more flowers in a given period of time. Conversely, if the crop is nectar-poor, bees forage more slowly and visit fewer flowers.

Directionality of bee foraging

Bees, having encountered a patch of profitable flowers, tend to forage in a more-or-less straight line. This behaviour limits the chance of a bee revisiting a flower recently emptied of its nectar (Pyke, 1978; Cresswell, *et al.*, 1995). The most straightforward implication for crop pollination involves those crops in which a main variety is interplanted

with one or more pollenizer varieties to ensure cross-pollination. Optimal foraging theory would suggest that the main varieties and pollenizers should be planted in the same orchard row to increase chances of bees cross-pollinating them.

Cues for identifying worthwhile flower visits

Bees use signals from plants to identify worthwhile visits. In some species the flowers remain open, intact and turgid until they are pollinated, after which they are no longer attractive to pollinators. The negative cues involved in this include cessation of nectar and scent production, change in colour, wilting, permanent flower closure, and petal drop (van Doorn, 1997). Even receptive inflorescences can vary in their attraction to bees. In general, inflorescences with a larger number of open flowers have higher nectar rewards, and bees preferentially land on those inflorescences. Once landed on an inflorescence, bees prefer wide, relatively shallow flowers, presumably because the nectar is more accessible to evaporation which concentrates it and increases the energetic profit of the visit (Duffield *et al.*, 1993).

These observations from ecological studies form the basis of a practical crop pollination recommendation. It is advisable for growers to delay the introduction of bee hives in an orchard until the crop has already begun a modest amount of flowering. This practice will provide bees with an abundance of floral signals that will encourage them to concentrate on the crop instead of non-target plants in the area. It is customary in apple to delay hive introduction until the crop is at about 5% bloom.

The Importance of Crop Attraction to Bees

Ecologic theory supports the notion that bee visitation and pollination are enhanced in plants that are attractive to bees. This was clearly the case for Pedersen (1953) who found in lucerne (alfalfa) a positive relationship between nectar production, bee visitation, and seed yield. Likewise, low nectar quality and associated low levels of bee visitation are limiting factors in fruit-set in avocado (Ish-Am and Eisikowitch, 1998). There is a clear and positive relationship among nectar sugar concentration, frequency of bee visitation, and resulting seed number in watermelon (Wolf *et al.*, 1999). Thus, theoretical work and supporting field studies strongly suggest that it is in the best interest of farmers to grow crop plants that are attractive to bees.

Nectar production is affected by ambient conditions and culturing practices, as shown by Shuel (1955) who worked with two model

plants, alsike clover and snapdragon. In these plants, nectar production is relatively high under conditions of low nitrogen supply, moderate growth, and high levels of sugar in tissues. It is lower under conditions of abundant nitrogen supply, high vegetative growth, and low sugar levels. Nectar production is generally higher in sunny weather because sugars accumulate in plant tissues during photosynthesis. These sugars may reach a surplus and be excreted as nectar if plants are not growing maximally. However, if nitrogen is available it encourages plant growth which diverts stored sugars into proteins and other products necessary for producing tissues. Thus, nectar production tends to be lower in plants that are growing rapidly. (In perennial plants that bloom before leaves unfold in spring, nectar production relies on sugars stored in tissues from the previous season (Bürquez, 1988).) The model of nectar production presented above is not universally applicable; for example, nectar production in the Mediterranean herbaceous perennial *Ballota acetabulosa* is relatively unresponsive to measured changes in solar irradiation (Petanidou and Smets, 1996).

There is evidence that nectar production also may be affected by plant genetics. There are measurable differences in nectar production within crop genera or species, as shown in pepper (Rabinowitch *et al.*, 1993), cranberry (Cane and Schiffhauer, 1997), and watermelon (Wolf *et al.*, 1999), and sometimes these differences are apparent even when environmental or cultural effects are controlled. These studies suggest that nectar production is at least partly under genetic control and could be increased by selective plant breeding.

The time is right to give renewed attention to increasing nectar production in the world's most important bee-pollinated crops. This is especially justified given the evidence for a generally decreasing pool of available bee pollinators (see Chapter 4). Nectar production has received comparatively little attention from crop breeders, agronomists, and horticulturists. Low nectar production may not be a problem in areas with abundant bee populations, but where bees are scarce a nectar-poor crop will have trouble competing with weeds for the limited number of pollinators.

Transgenic Crops

One of the most recent, controversial, and potentially revolutionary areas of agricultural research is the development of genetically engineered, or so-called transgenic crops. Genetically engineered organisms are ones in which genes from different species have been inserted in such a way as to permit those genes to express their characteristics in the host organism. In crop plants the focus has been on inserted genes from the bacterium *Bacillus thuringiensis* that trigger

production of insecticidal compounds in the tissues of the host plant. The number of different transgenes that have been used to confer insect resistance in crops approaches 40 (Schuler *et al.*, 1998), but only *B. thuringiensis* transgenes have been commercialized. Transgenes also have been used to confer herbicide tolerance, drought or salt tolerance, or to alter the nutritional qualities of the crop. The relevance of pollinators to transgenic crop technology rests on two issues – the potential harm to pollinators posed by transgenic crops, especially insecticidal ones, and the potential harm to the environment caused by pollinators spreading transgenes into wild plant populations.

Transgenic insect resistance is seen to have numerous advantages over conventional insecticides. It provides more targeted delivery of a toxin to the pest, greater resilience of the toxin to weather or other forms of biodegradation, reduced exposure risk to the applicator, and reduced use of conventional broad-spectrum insecticides and their associated risks to the environment (Schuler *et al.*, 1998). But there has been concern that engineered toxins, whether in the plant's tissues or in its nectar and pollen, could be detrimental to bees. Fortunately, that risk seems small at this time. A sizeable research record has shown that *B. thuringiensis* toxins, whether conventional or engineered, are generally benign to bees (Poppy, 1998). The risk from other candidate engineered toxins, namely the pesticidal proteins chitinase, β-1,3glucanase, and cowpea trypsin inhibitor (CpTI), likewise seems small as shown by honey bee toxicity studies performed by Picard-Nizou *et al.* (1997).

Another area of concern with this new technology has been the potential of transgenes 'escaping' from engineered crops into wild plant populations with unknown and perhaps detrimental effects. Chief among these concerns is the potential for transgenes for herbicide tolerance becoming incorporated into weedy species, thus making them more difficult to control. Bees, because of their pollen-collecting habit and catholic flower preferences, are seen as primary vehicles for the spread of such transgenes. One solution to the problem may be a buffer zone of conventional crop plants grown around the transgenic ones. Pollinators visiting the transgenic plants may subsequently deposit much of their plant-available pollen on to conventional crop flowers in the buffer zone before leaving the area to visit other plant species or to return to the nest. It is unlikely that buffer zones alone will solve the problem in all cases. In one study, honey bee colonies were placed at a distance of 250 m from a field of transgenic herbicide-tolerant maize. The transgenic field was surrounded by a 3 m buffer zone of conventional maize. Of the pollen samples collected from the colonies, 52% contained the transgene for herbicide tolerance; thus the 3 m buffer zone did not prevent the

spread of the transgene (Reiche *et al.*, 1998). There is evidence that most of the pollen from a particular plant is deposited by a bee forager on to the next few subsequent flowers visited, but some pollen can persist for up to the 20th subsequent flower (Cresswell *et al.*, 1995). Ongoing research is concentrating on gene flow from transgenic crops, the competitiveness of transgenic plants, the efficacy of isolation distances, and the interactions of bee foraging behaviour with pollen movement among plants (Poppy, 1998).

Chapter 3

Bees: An Overview

General Bee Biology

Bees belong to the insect order Hymenoptera which also includes the sawflies, ants, and wasps. Unlike other hymenopterans, bees tend to specialize on exclusively vegetarian diets. Both immature bees and adults eat plant-derived pollen for protein and nectar for energy. Some social species feed their young glandular secretions produced by nurse bees, conceptually like lactating mammals. But even these secretions are metabolically derived from pollen and nectar. Some social bees with long-lived colonies dehydrate nectar into *honey*, a process which preserves the nectar for long-term storage.

Bees have body features that further distinguish them from other insects. Many of the body hairs on bees are finely branched so that pollen grains cling to them readily. Most bees have external body structures specialized for carrying pollen. With some, a segment of each hind leg has a structure called the *corbiculum* or *pollen basket* for holding loads of pollen while the bee is foraging. Others carry pollen on long hairs attached to their hind legs. One group carries pollen loads on the underside of the abdomen. Bees' pollen-carrying capabilities and flower-visiting habit make them one of the most important crop pollinators worldwide.

Developing immature bees go through a *complete metamorphosis* (Fig. 3.1). Individual bees start life as a single *egg* laid by their mother. After a few days the egg hatches into a *larva* (plural *larvae*) which is a grub-like, rapidly-growing feeding stage. As they grow, larvae shed their skin several times by a process called *moulting* to advance to the next larger stage, or *instar*. Eggs are laid and larvae develop in cells varying in complexity, ranging from hexagonal beeswax cells to simple dead-ends in earthen tunnels. The mother or siblings provision each larval cell with food. Some species add pollen and nectar to the cell regularly as the larva needs it; others feed it all at once as a large,

moist lump at the time the egg is laid. Because bee larvae literally live in their food, defaecation is a problem. Larvae solve this by postponing defaecation until their feeding career is over. When it completes its feeding period, the larva defaecates, stretches out (then called a *prepupa*), and transforms into a *pupa* (plural *pupae*) which is a quiet stage during which larval tissues are reorganized into those of an adult. Finally, the pupa moults into an *adult*, complete with six legs and four wings, and breaks out of its cell. Species vary in the amount of time immatures spend in each stage.

Female bees control the sex of their offspring. They store sperm from their matings in the *spermatheca*, an organ connected to the *oviduct* which is the passage down which eggs pass during oviposition. Females have muscular control over the spermatheca. By opening it and releasing sperm on to a passing egg, the female can fertilize the egg and the result is a female. Unfertilized eggs result in males. This ability to regulate sex of offspring is important in solitary tunnel-nesting bees because they tend to lay male eggs near the nest entrance so males can precede the females in spring emergence. For social species it is important to time male production according to seasonal food availability.

The adult stage of bees is dedicated to dispersal and reproduction. Bees do this with a variety of life strategies and nesting habits, ranging from solitary to social, from simple burrows to elaborate comb nests.

Solitary versus Social Bees

There are about 25,000 described species of bees in the world (O'Toole and Raw, 1991). Most are *solitary* species in which females

Fig. 3.1. Bees undergo complete metamorphosis, progressing from the egg stage to the larva, to the pupa, and finally the adult. (Source: Darrell Rainey.)

singlehandedly make a nest and produce the next generation of fertile offspring. Most solitary species produce only one or two generations per year.

Social species live together as a colony of related individuals in which there is: (i) cooperative care of the young; (ii) more-or-less infertile female workers; and (iii) offspring that stay at the nest to help their mother produce more siblings (Wilson, 1971).

In social species, individuals of the same sex occur in different sizes and forms called *castes*. The *queen* is a female fully equipped to mate and lay fertilized eggs that become female workers or queens. *Workers* are females that do not mate but on occasion do lay unfertilized eggs that become males. Workers do most of the house cleaning, brood nursing, temperature regulating, foraging, and defending for the colony. Male bees, sometimes called *drones*, are visibly distinguishable from workers and queens; their only known function is to mate with queens. Both solitary and social species can be important crop pollinators.

Honey Bees versus Other Bee Species

For crop pollination purposes, bees are more easily distinguished as either *honey bees* or *non-honey bees*.

'Pollen bees' is a recently-coined term intended to include all pollinating bees that are not honey bees (Adams and Senft, 1994). Bees in this group concentrate on collecting pollen compared to the honey bees that collect large quantities of nectar. The term pollen bees is aesthetically more pleasing than other choices (i.e. 'non-honey bees'), but it is ambiguous because both honey bees and pollen bees collect pollen and pollinate crops. Plus, the life histories and management of pollen bees are so diverse that the term quickly loses descriptive usefulness. We prefer the terms 'honey bees', 'non-honey bees' (includes managed and non-managed species), and 'non-managed bees' (includes wild populations of honey bees).

Most non-honey bees have relatively simple life cycles and make simple burrows in wood, grass thatch, hollow stems, or soil and produce, at most, only a few offspring. One exception across much of the temperate developed world is the social bumble bees that make complex comb nests and colonies with several hundred individuals. Culturing and management methods for some non-honey bees are well developed and covered in Chapters 8–12.

Compared to honey bees, non-honey bees can pollinate certain crops more efficiently because of their distinctive behaviours, morphology, or life habits (Kuhn and Ambrose, 1984; Cane and Payne, 1990). Bumble bees and others *sonicate* or *buzz-pollinate* blossoms by

shaking pollen from the flower with high-frequency muscle vibrations; this improves pollination efficiency in relatively closed flower structures such as blueberry and tomato. Some non-honey bees have longer tongues than honey bees and this enables them to pollinate tubular flowers, such as red clover, more effectively. The strongly seasonal life history of many solitary bees serves in some cases to enhance their effectiveness as pollinators. These bees have a simple life cycle in which adults emerge, fly, mate, and provision brood cells during the few weeks of peak bloom in their area. Thus many solitary bees are specialists for those plants blooming during their brief flight season, and this specialization works in favour of the grower if those plants are flowering crops. Social honey bees and bumble bees, on the other hand, visit many flowering plants over the course of a season. They are generalists, not specialists, and they are more easily lured away from the crop of interest. The urgency with which solitary bees must work during their short active season also works in favour of the grower; compared to honey bees, non-honey bees often work longer hours, work faster, visit more blossoms per day, and fly more readily during inclement weather.

Solitary bees are generally less likely to sting than are the social honey bees and bumble bees. Bee handlers who propagate solitary pollinators such as alkali bees, alfalfa leafcutting bees, and orchard mason bees routinely do so with little or no sting-protective clothing.

There are also disadvantages and uncertainties with non-honey bees and non-managed bees. First, non-honey bees pollinate several crops more efficiently than honey bees on a per-bee basis, but no study has accounted for the overwhelming population advantage of honey bee colonies. Honey bees produce the largest colony population sizes of any bee species. Conceivably, one honey bee colony, with thousands of inefficient (for argument's sake) pollinators could match or exceed many nests of efficient, but solitary, bees (see Corbet *et al.*, 1991, for an experimental design to determine the pollination value of a given bee species). Populations of non-managed bees are often too small to support commercial pollination needs (Morrissette *et al.*, 1985; Parker *et al.*, 1987; Scott-Dupree and Winston, 1987) or vary considerably between years and geographic regions (Cane and Payne, 1993). Just like honey bees, non-honey bees have diseases, predators, and parasites that limit their natural populations or, for managed populations, must be controlled by the bee-keeper. Nevertheless, where they occur in sufficient numbers, whether through favourable habitat, mass introductions, or culturing, non-honey bees can replace or supplement honey bees for commercial pollination in some crops.

In this book, we cover seven groups of pollinating bees that are important in the temperate developed world, especially North America: honey bees (Chapters 5, 6, and 7), bumble bees (Chapter 8),

alkali bees (Chapter 9), other soil nesting bees (Chapter 10), alfalfa leafcutting bees (Chapter 11), orchard mason bees (Chapter 12), and carpenter bees (Chapter 13).

Effects of Non-Native Bee Species

Human beings have moved many species of bees outside of their native ranges, some accidently and some intentionally. Chief among these is the European honey bee *A. mellifera*, but included in their ranks are other well-known pollinators such as the European bumble bee *Bombus terrestris* (Chapter 8) and alfalfa leafcutting bee *Megachile rotundata* (Chapter 11).

Honey bees successfully established robust feral populations in most temperate habitats into which they were introduced. This background of feral honey bees was credited with a significant portion of crop pollination until more recent years when the spread of parasites, primarily varroa mites, severely reduced their numbers. Some authors have also credited exotic honey bees as pollinators of native plants that in turn support populations of wildlife, essentially asserting that exotic honey bees are an asset to local ecosystems (Barclay and Moffett, 1984). Other authors have voiced concern that introduced honey bees are not entirely benign and may in fact displace native bees, disrupt pollination of native plants, and help propagate introduced weeds (reviewed by Butz Huryn, 1997). Evidence can be found for either position; however, the bulk of experimental evidence fails to demonstrate any general and large-scale detrimental effects of exotic honey bees (Butz Huryn and Moller, 1995; Butz Huryn, 1997; Horskins and Turner, 1999). The fact that the foraging behaviour of honey bees does not differ qualitatively from that of many other bee taxa (Butz Huryn, 1997) indicates that honey bees can pollinate many native plants effectively, as suggested by the data of Horskins and Turner (1999) with native *Eucalyptus costata* in Australia.

Since the 19th century, the European bumble bee *B. terrestris* has been exported from its native range into several countries including Australia, New Zealand, the Philippines, South Africa, Mexico, Japan, China, Korea, and Taiwan as part of efforts to improve crop pollination in those countries. Its expansion has accelerated in recent years as a result of a growing export market for cultured bumble bee colonies for glasshouse pollination. By this means, populations of *B. terrestris* are known to have escaped from commercial cultivation and invaded natural habitats in Japan and Tasmania (Dafni, 1998). As with introduced *A. mellifera*, there are conflicting opinions about the effects of these introduced bees on native flora and fauna. Donovan (1980) concluded that *B. terrestris* is not a significant competitor with

native New Zealand bees because it occurs at relatively low densities and spends comparatively little time on native flowers. However, in Tasmania it has been shown that *B. terrestris* does forage across a wide selection of native flowers and at densities sufficient to competitively displace native bees (Hingston and McQuillan, 1998, 1999). Likewise, there is evidence in Israel that *B. terrestris* is expanding from its natural range limit in the northern part of that country and competing with native bees for limited resources (Dafni, 1998).

The alfalfa leafcutting bee was introduced to South Australia from New Zealand in 1987 in an effort to augment pollination of lucerne grown in the area. In a survey during the 1988/89 lucerne growing season, no introduced leafcutting bees were detected on nearby native plants and there was no measurable dispersal by bees away from the release sites; thus, the impact of the bees on the natural ecosystem appeared negligible (Woodward, 1996).

Appraising the assets and liabilities of introduced pollinators is a difficult and controversial issue. It inevitably pits the economic assets of the bees as crop pollinators against their ecological liabilities as exotic species. It is naive to think that introduced bees have had no effects on native plants and animals, but the bulk of experimental evidence suggests that the effects have been, in the main, relatively subtle. Perhaps if there were more research on the matter the accumulated evidence would indicate otherwise. Nevertheless, it seems prudent to point out that many of the important crop plants grown around the world today are themselves exotic species growing outside of their native ranges. In this context, the parallel export of crop pollinators appears less monstrous.

Chapter 4

Bee Conservation

Bees as a Limited Natural Resource

In the late 20th century scientists and other observers began asserting that the rate of species extinctions across many plant and animal groups is increasing at an alarming rate (Wilson, 1992). This opinion is not universal (Simon and Wildavsky, 1992), but in the case of bees there are studies that suggest a loss of species diversity in some localities. This is cause for concern especially when considering the profound value of bees to human economies and well-being (see Chapter 1). Moreover, bees are crucial to the functioning of almost all terrestrial ecosystems to the extent that the robustness of their populations and species richness can serve as bioindicators of the state of local environments (Kevan, 1999). The blame for species loss, whether in bees or other organisms, has been laid at the feet of a hundred causes – deforestation, pollution, poaching, pesticides, urbanization, invading exotic species, to name a few. Habitat destruction, loss of blooming food plants, and spread of parasites and diseases are the environmental perturbations most likely to adversely affect bees.

Across North America, there has been an unprecedented decline of wild honey bees in recent years. Winter losses in a population of feral honey bees in southern Arizona increased from 13% in 1991/92 to 61% in 1994/95 (Loper, 1995), and the number of feral colonies in an area near Sacramento, California declined 75% between 1993 and 1990 (Kraus and Page, 1995). The main culprits for these losses are two exotic honey bee parasites that entered the US in the 1980s: the tracheal mite (*A. woodi*) and varroa mite (*Varroa* sp.).

The number of managed honey bee colonies is also declining in some developed countries. Between 1943 and 1996 the estimated number of managed honey bee colonies in the UK dropped from 429,000 to 200,000 (Butler, 1943; Carreck and Williams, 1998).

Bee-keeping in North America has also declined as bee-keepers suffered setbacks in recent years that threaten the long-term sustainability of a honey-bee-based pollination industry. Profitability declined as the US government pared away subsidies for honey producers. Tracheal mites and varroa mites kill untold thousands of colonies annually and are expensive to control. Highly defensive Africanized bees may infiltrate bee stocks in parts of the continent and motivate bee-keepers to leave the business. It is perhaps no surprise that the number of bee-keepers in the US dropped by about 20% between 1990 and 1994 (Watanabe, 1994). It may become increasingly difficult to get enough honey bees to satisfy commercial pollination needs. This already seems to be the case in California almonds (Burnham, 1994), avocados (Mussen, 1994), in Florida citrus (Sanford, 1994), and in Washington orchard fruits (D.F. Mayer, personal observation).

In Europe, declines of bumble bees and other non-honey bees are documented in Britain (Williams, 1982, 1986), Lithuania (Monsevičius, 1995), Turkey (Özbek, 1995), Belgium and northern France (Rasmont, 1995), and parts of Poland (Ruszkowski and Biliński, 1995), although in western Poland the number of bee species remains virtually unchanged since the 1940s (Banaszak, 1992).

Populations of non-honey bees, whether natural or managed, are vulnerable to loss from many causes. Numbers and species diversity of bees are generally higher in natural vegetation than in disturbed agricultural areas, as shown in British Columbia (MacKenzie and Winston, 1984) and in Massachusetts (MacKenzie and Averill, 1995). Man's activities destroy bee habitat and forage. Vast monocultures of exotic crops, especially non-nectar-bearing cereals, can displace native bee forage. Pesticides applied to flowering plants, forest foliage, or bee nesting sites can reduce local populations. For example, native bee populations in New Brunswick took three years to rebound after fenitrothion was applied on nearby woodland to control spruce budworm (Wood, 1979). Similarly, managed alkali bee (*Nomia melanderi*) populations in Washington took 3 years to rebound after an application of diazinon (D.F. Mayer, personal observation).

Managed alfalfa leafcutting bees (*M. rotundata*) in the western US and Canada are attacked by fungi, predators, and insect parasites. A similar bee species, *Megachite apicalis*, does not prefer lucerne and sometimes takes over nests of the economically important *M. rotundata* (Peterson *et al.*, 1992). Fortunately, fumigation, sanitation, and insecticide-application procedures to control some of these diseases and pests are available (Goerzen and Watts, 1991; Mayer *et al.*, 1991, 1992; Goerzen and Murrell, 1992; Goettel *et al.*, 1993).

It is suggested that the exotic honey bee also may contribute to a decline of native non-honey bees (Buchmann and Nabhan, 1996).

Indeed, in the three centuries since its introduction to North America, honey bees have competed successfully with native pollinators for food resources. Honey bees excel at finding the richest nectar sources in a habitat which they then preemptively deplete, leaving behind less for non-honey bees (Ginsberg, 1983; Schaffer *et al.*, 1983). It has been estimated that one honey bee colony can, in this manner, competitively reduce the number of bumble bee queens and males produced within its foraging area by as much as 38,400 (Heinrich, 1979). Nevertheless, it has proven difficult to empirically demonstrate a negative environmental impact of introduced honey bees (see page 22).

Bumble bees occasionally are attracted to honey bee nests, and if they enter them they are often killed (Thoenes, 1993). A large number of these killed invaders are reproductive queens and males (Morse and Gary, 1961).

The perception of a bee shortage also may stem from a sharp worldwide increase in the area of bee-pollinated crops at the expense of cereals (Osborne *et al.*, 1991). Even undisturbed healthy bee populations may not be large enough for the enormous task an expanding human population now asks of them.

Clearly, it is in society's best interest to maximize the number and diversity of our crop pollinators. This includes all bee pollinators, honey bee and non-honey bee alike. For honey bees, more research is needed to improve parasitic mite control, improve profitability, and contain costs of production. Honey bees are manageable, adaptable, prolific, and effective for many crops, benefits that cannot be dismissed or marginalized. For non-honey bees, research is needed to understand basic life histories, develop or perfect culturing methods, and identify suitable food plants and nesting sites for conservation programmes. Finally, private and public granting agencies must recognize the importance of abundant pollinators and appropriately fund research and education programmes to that end.

Bee habitat conservation and improvement have received considerable attention in Europe, but relatively little in North America. Conservation, however, is conceivably one of the most cost-effective ways to increase pollinators. The changes brought about by conservation programmes, such as habitat sanctuaries and perennial bee pastures, tend to be long-lasting, spreading the cost of their installation over many years. Moreover, the benefits are long-lasting since permanent nesting sites and pastures encourage large, locally-recurring bee populations. In this chapter we highlight some of the principles and practices of bee conservation. Information given here was constructed largely in the context of conserving wild non-honey bees, but the practices recommended can indiscriminately benefit non-honey bees and honey bees alike.

Habitat Conservation

The information in this section is intended to assist one in appraising the conservation value of lands and in identifying and implementing steps for improving them for bees.

A self-sustaining bee population requires long-lasting, undisturbed nesting sites and plants that annually produce nectar and pollen during bee nesting seasons. These facts are the foundation of any bee conservation programme. A self-sustaining bee population also needs some ecologic refuge against predators, parasites, and diseases. In practice, bee conservationists focus on enhancing nesting sites and food plants because there is little they can do about predators and parasites of natural bee populations. This is not the case with managed bees.

Characteristics of good bee habitats

Osborne *et al.* (1991) ranked some habitat types in central and Atlantic Europe for their suitability for bees (Table 4.1). Their ranking is based on the nesting sites and plant types available in those habitats and

Table 4.1. Ranking of some European habitats for their suitability for bee forage and nesting sites (Osborne *et al.*, 1991).

Ranking	Atlantic Europe	Central Europe
1 (best)	Calcareous (limed) grasslands	Wet meadows
	Heaths[a]	
2	Fens[b]	Fens
	Hedges[c]	Heaths
	Wastelands	Fresh meadows
	Neutral grasslands	
	Woodland edges	
3	Bogs[d]	
	Marshes	
	Wastelands	
4	Oak woods	Oak woods
	Ash woods	Alder woods
	Moorlands[e]	Some beech woods
5 (worst)	Beech woods	Beech woods
	Conifer woods	Conifer woods

[a] Open, barren land with acidic, poorly-drained soil and shrubby plants.
[b] Lowlands covered wholly or partly in water, unless drained.
[c] Dense shrubbery at field margins.
[d] Wet, spongy, acidic soil with a characteristic flora.
[e] Open, rolling, boggy wasteland dominated by grasses and sedges.

illustrates some general features of habitats that have universal significance in bee conservation.

From Table 4.1 we can illustrate some important principles and practices for bee habitat conservation. First, it is apparent that bee activity and reproduction are optimized in open, sunny habitats with an abundance and diversity of food plants, in contrast to those in flower-poor, shaded woodlands. Warm, sunny, relatively bare patches of ground are preferred nesting sites, in part because warm conditions speed the development time of immatures and promote flight activity of adults. This is especially important for annual nests of solitary bees and bumble bees and helps explain why soil-nesting bees often dig nests in patches of soil with a southern aspect that maximizes exposure to the sun (Potts and Willmer, 1997). Second, as the diversity of nectar- and pollen-bearing plant species increases, the diversity of bee species in a habitat also increases (Banaszak, 1983). Unfortunately, modern agriculture tends to promote the exact opposite type of habitat – large monocultures, frequently of cereals or other nectar-poor plants. If the monoculture happens to be a good bee forage, then there may be many bees but the number of bee species will tend to be low. Honey bees are the most likely bee visitors in these cases since they excel at exploiting rich food resources (Schaffer *et al.*, 1983). The reverse of this situation is natural habitats which may have a smaller density of plants but whose diversity of plant species will support a more diverse bee fauna.

The increase in pine forest monocultures in North America does not bode well for bee populations except in those areas with good nectar-producing understorey and margin plants such as bramble, gallberry, and palmetto. Trees such as red maple, sourwood, and tulip poplar are good pollen or nectar sources, but even in these types of forests the bees are more likely to nest at the forest margins that have sun and a variety of nesting sites and flowering plants.

At this point we can generalize that for ground-nesting solitary bees or bumble bees, land conservation efforts should focus on sunny, open undisturbed meadows, field margins, sun-drenched undisturbed patches of bare soil, roadsides, ditch banks, and woodland edges. In any year, a farm can have large areas of such idle land, and using it for bee sanctuary costs next to nothing and involves mostly a willingness on the part of the land owner to leave it undisturbed for the long term. By 'undisturbed' we mean no draining, herbicides, ploughing, or compacting with heavy machinery. Maintaining such undisturbed areas will increase the abundance of bee nesting sites and diversity of flowering plant species on farms. The presence of such bee sanctuaries in the agricultural landscape of western Poland is one reason Banaszak (1992) gives for the surprising constancy of bee diversity there over 40 years. Another reason was plantings of agronomic crops that are very rich bee forages, namely lucerne, clover, oilseed rape, and sunflower. These rich forages can partially compensate for lost diversity of native plants.

The importance of habitat permanence

The richness of plant and bee species in undisturbed fallowed fields increases with time (Gathmann *et al.*, 1994). This means that one should plan bee sanctuaries for the long term. As the years go by a land manager can expect increasing numbers of plant and bee species in these undisturbed sanctuaries. But one catastrophic event, such as ploughing, can undo years of progress.

Mowing management

The most effective bee sanctuaries are mid-successional plant communities, having an abundance of herbaceous perennials and few or no invading trees (Dramstad and Fry, 1995). Biannual mowing is advisable to keep a sanctuary from succeeding into shaded woodlands or scrub lands. It is best to mow in winter when it is less likely to destroy active bumble bee colonies. A light mower is preferable to a heavy tractor-mounted implement that may crush nests of overwintering soil-nesting bees.

Livestock pasture management

Pastures used for hay or animal grazing are generally inhospitable to bees, but there are ways to manage them in a manner consistent with a bee conservation programme (Osborne *et al.*, 1991). One way to do this is to make pastures more-or-less permanent. The older the pasture, the more likely it is to have suitable bee nest sites and numerous plant species. Temporary pastures, such as those grown in crop rotation, have very low plant diversity even though the cover crop may be a rich resource for one season. Overgrazing is inadvisable because it promotes invasion of fast-growing grasses that crowd out nectar-yielding herbaceous plants. Herbicides similarly can reduce the number of pasture plant species. It is preferable for land managers to delay cutting pasture for hay until after a certain period of bloom. Cutting forage plants before they bloom essentially renders the pasture nutritionally useless to bees.

The importance of nesting materials

An ideal bee habitat must also provide nesting materials (mud, leaves, etc.) appropriate to the needs of a particular bee species. For example, a shortage of mud could be a limiting factor with orchard mason bees

(*Osmia* spp.), a group that uses mud in nest construction. Bumble bees need grassy thatch or abandoned rodent burrows in which they build their nests. If a local bee sanctuary meets the more important general standards discussed above, appropriate nesting materials will probably follow suit, but the matter should not be disregarded. One commercial blueberry grower in south Georgia, USA set out shelled maize under sheets of plywood around his orchard in an attempt to increase the number of rodent nests in the area which, in turn, would provide future nest sites for pollinating bumble bees.

Habitat Improvement with Bee Pastures

Bee conservation can go beyond habitat preservation, which is essentially a passive process, to active habitat improvement through the establishment of permanent bee pastures. The goal is to provide a reliable source of quality nutrition which will serve to increase bee numbers, either by attracting bees to the area, increasing the number nesting in the area, or by increasing their reproductive output. Benefits of perennial pastures can be long-lasting since non-honey bees tend to nest near where they were reared the previous year (Butler, 1965; Osborne *et al.*, 1991). Measured against the background of normally-occurring food plants, the installed pasture must be large enough and rich enough to positively affect bee populations; these are threshold values knowable only by research, ideally conducted on a local basis.

The idea of installed bee pasture is not new and, in fact, has strong support from the scientific literature. Most of the work has involved bumble bees, and indeed it is bumble bees that have the most to gain from such a programme. Solitary bees, with their relatively short active seasons, are most beneficial if they spend their foraging careers on the crop of interest, and honey bees, with a perennial life cycle and large food stores, can overwinter and reproduce tolerably well even if their habitats subject them to long periods of food shortage. But bumble bees, with an annual life cycle and small food stores, need a season-long progression of food plants in order to reproduce.

The literature contains voluminous references to bee and flower associations. Much of it is intended to identify promising honey plants for honey bee-keepers (Pellett, 1976; Crane *et al.*, 1984; Ayers *et al.*, 1987; Sanford, 1988; Ayers and Harman, 1992; Williams *et al.*, 1993; Wroblewska *et al.*, 1993; Villanueva-G, 1994). Even so, many of these lists are helpful to conservationists.

Conservationists are primarily interested in identifying assemblies of plants that are nutritionally useful to bees, easy to grow, cost-effective, non-invasive, bloom over a long period of time, and do not com-

pete with the crop for pollinators. Some researchers have identified bee pasture plants for particular agricultural settings. Fussell and Corbet (1991) identified naturally-occurring bee plants in field bean and oilseed rape farmland in the UK. Patten *et al.* (1993) screened 21 herbaceous plants for their suitability as bee pasture near cranberry bogs in the northwestern USA. Krewer *et al.* (1996) identified eight candidate plants for supplemental bumble bee pasture near rabbiteye blueberry orchards in Georgia. This kind of work is necessarily localized because bee plants championed by one author in one region sometimes disappoint another (for example, Mayer *et al.*, 1982, versus Ayers *et al.*, 1987, concerning anise hyssop), and there are obvious geographic differences in plant hardiness zones and flowering times. Finally, bee species differ in flower preferences, often based on the morphological match between flower parts and bee mouth parts (Fairey *et al.*, 1992; Patten *et al.*, 1993; Plowright and Plowright, 1997). We will now summarize some important principles and practices for bee pasture plantings.

The importance of season-long bloom

The value of bee pastures to local bee populations is optimized in those pastures that have a season-long succession of bloom. This principle is best illustrated with bumble bees. With an annual life cycle, the top priority of a bumble bee colony is to produce a new crop of mated queens for the following season. Each colony has only a few weeks to start a nest (as a solitary queen), rear a foraging force of workers, and collect enough food to produce new queens and males. The number of queens a colony can produce depends largely on the number of workers it can produce in the weeks leading up to the queen production period (Heinrich, 1979). Producing workers requires energy, so a colony's reproductive success ultimately hinges on season-long availability of food. The link between good nutrition and high queen output was underscored by Bowers (1986) who showed that new queens appear earlier in those meadows with the richest flower densities.

Mid-summer nectar dearths can be disastrous. Again, bumble bees illustrate the magnitude of this problem. Unlike honey bees that store large surpluses of food, bumble bees store enough nectar for only a few days at most. This makes them vulnerable to nectar dearths. Worker bumble bees stop incubating brood and respond lethargically to invading predators and parasites in colonies that are experimentally deprived of nectar for even one day (Cartar and Dill, 1991). Therefore, a mid-season nectar dearth can be a simple matter of life or death, let alone a compromise on reproductive performance.

These principles lead us to conclude that in planning a bee pasture one should choose a collection of plants so that there is an unbroken succession of bloom throughout the season. The first step is to identify the normally-occurring bee plants in one's area and their historic bloom periods, information readily available from local honey bee-keepers. Once dearth times in the natural bloom calendar are identified, the next step is to select bee pasture plants that bloom historically during those dearth times. Local extension specialists, horticulturists, nursery stock growers, and published bee plant lists are helpful in making these selections. It is important to avoid plants that bloom at the same time as the crop of interest or are invasive or otherwise noxious.

The commercialization of seed blends designed to produce a succession of bloom has been realized in Europe largely in response to the EU's land set-aside programme enacted in 1988. By 1994 the set-aside programme had resulted in 781,000 ha of arable land being removed from production in the UK alone (Carreck and Williams, 1997). This idled land represents an enormous opportunity to grow food plants for bees, and seed blends are commercially available that have been designed to provide a succession of bloom on lands designated for one-year set-aside. Two of these blends are the Tübingen Mixture (Bauer and Engels, 1992; Engles *et al.*, 1994) and the Ascot Linde SN mixture (Cebeco Zaden BV, Vlijmen, The Netherlands and Stichting Imerij Fortmond, Olst, The Netherlands). The composition of the Tübingen Mixture is as follows: 40% phacelia (*Phacelia tanacetifolia*), 20% buckwheat (*Fagopyrum esculentum*), 7% white mustard (*Sinapis alba*), 6% coriander (*Coriandrum sativum*), 5% marigold (*Calendula officinalis*), 5% caraway (*Nigella* spp.), 5% sunflower (*Helianthus annuus*), 3% red radish (*Raphanus sativus*), 3% cornflower (*Centaurea cyanus*), 3% mallow (*Malva sylvestris*), 2% anethum (*Anethum graveolens*), and 1% borage (*Borago officinalis*). The availability of seed blends of annuals such as these is certainly applaudable and is conducive to the adoption of bee conservation practices by farmers. However, prepared blends may not replace locally designed plant assemblies. Working with the Tübingen and Ascot Linde SN mixtures in the UK, Carreck and Williams (1997) found that phacelia dominated in terms of establishing, flowering, and attracting insects and that the other plants contributed little to bee diversity.

The importance of perennials as bee pasture plants

Another principle important in planning bee pastures is that perennial plants are generally to be preferred over annuals. Although some annuals provide rapid and relatively abundant bee forage, perennial

herbs and shrubs are generally superior forages and preferred by bees (Parrish and Bazzaz, 1979; Fussell and Corbet, 1992; Dramstad and Fry, 1995; Petanidou and Smets, 1995). Compared to annuals, perennials are richer nectar sources owing, in part, to their ability to store and secrete sugars from the previous season. Perennials provide bee populations with a more-or-less dependable food source year after year and encourage repeated bee nesting in the area. This is an important factor explaining why the number of bee species and plant species tends to increase together over time in undisturbed meadows. Thus, we can generalize that whenever possible bee pastures should be stocked with perennial bee plants. Considering the repeated labour and inputs required for annuals, perennials are a cost-effective, low-maintenance choice for growers installing bee pasture.

It is important to remember that bee nesting and foraging activities centre on flower-rich habitats. There is evidence that bumble bee queens prefer to nest in flower-rich meadows (Bowers, 1985). The foraging range of most non-honey bees is probably smaller than that of honey bees (Osborne *et al.*, 1991), although this may not always be the case with bumble bees (Dramstad, 1996; Saville *et al.*, 1997; Osborne *et al.*, 1999). All things considered, it seems most advisable to place bee pastures as near as possible to the crop of interest. This increases the chance of bees nesting near to, and foraging on, the crop. Working with candidate bee pasture plants on cranberry farms, Patten *et al.* (1993) recommended 'a sequence of early blooming forage plants adjacent to [cranberry] bogs' to encourage bumble bee nesting near the crop.

In most cases, installed bee pastures should be designed so that pasture plants do not bloom at the same time as the crop of interest and thereby compete with it for pollinators. However, not all bloom overlaps are harmful. Some highly-attractive flowering plants, called *magnet species*, can attract large numbers of pollinators to a plant (crop) community (Thompson, 1978). With *facilitation* or *spill-over* pollination (Laverty, 1992), the rate of pollinator visitation in a crop is augmented due to the presence of nearby blooming magnet species, as shown by Brookes *et al.* (1994) in Canadian lucerne.

Not all experts agree on the value of establishing bee pastures, or bee sanctuaries in general. Torchio (1990a) questions whether such 'reconstituted habitats' are cost-effective in areas of intense agriculture and high land values. He further points out that habitat management programmes rarely address the problems of reintroducing and maintaining entire bee communities in areas from which they have become extinct. These are valid questions and must be addressed before bee habitat management programmes gain wide acceptance.

Nevertheless, we believe that bee conservation has the potential to be an important component of an overall agricultural land use policy. Conservation efforts are well grounded in ecologic theory and supported

by studies that consistently link high bee diversity with large, undisturbed, florally-rich, long-blooming habitats. It remains to see if conservation programmes will practically and profitably translate into large and sustainable pollinator populations at the local level.

The Importance of Large Conservation Areas

As land use managers consider the idea of bee sanctuaries and pastures, it is important to think on a geographically large scale. The diversity of bee species is highest in large, continuously-connected areas of suitable habitat. Unfortunately, farming and urbanization tend to produce the exact opposite – small fragments, or 'islands' of suitable habitat widely separated by large tracts of inhospitable landscape. When there are many edges to a species' natural habitat, there is an increased risk of invasion by competitors and parasites and predators, a decrease in the species' ability to disperse, and an increase in its rate of inbreeding. On the other hand, some exotic species flourish on such edges. In forest bee habitats in Argentina, the exotic honey bee is the most common flower visitor in small forest fragments, whereas the occurrence of native bees increases in large unbroken forest (Aizen and Feinsinger, 1994). Differences were apparent on the scale of acres; small forest fragments (< 2.5 acres, < 1 ha) had fewer bee species visiting flowers than did larger forest fragments (> 5 acres, > 2 ha) which had fewer species than continuous forest. These authors expressed concern that unchecked forest fragmentation could ultimately replace the locally-rich assembly of bee species with one 'jack-of-all-bees' – the honey bee. Another study showed that queen bumble bees searching for nest sites in early spring prefer to colonize large meadows over smaller ones (Bowers, 1985).

The primary message from these studies is that bee conservationists should aim for sanctuaries as large as possible. One large, connected bee sanctuary, ideally on a scale larger than that of an individual farm, is better than several small, disconnected sanctuaries. Banaszak (1992) recommended that the area of land in cultivated fields or mowed meadows should not exceed 75% of the total area in a normally functioning agricultural landscape. The remaining 25% should be left as bee sanctuary.

Bee Conservation and Plant Conservation

Altered habitats are prime causes of plant species loss. Plants whose habitats become fragmented are widely separated from each other and may have trouble attracting pollinators. This seems to be the case with

some wildflower species in Europe (Corbet *et al.*, 1991). One can imagine the vicious cycle at work here: habitat fragmentation separates the plants from their pollinators; plant numbers decline for lack of pollinating bees; bee numbers decline for lack of food plants.

Some agricultural practices also may rob native plants of habitat and lure away their pollinators. Williams *et al.* (1991) speculate that vast monocultures of bee-attractive crops may lure all bees, native and exotic, away from native plants, depriving them of pollination and contributing further to their decline.

Bee conservation goes hand in hand with conservation of the plants that depend on them for pollination. Without their pollinators, the colourful bee-pollinated plants that beautify our surroundings, control erosion, and increase our property values would decline with unknown effects on the wildlife that depends on them for food. Thus, bee conservation is not just an issue for bee-keepers and crop growers, although food production is by far the most important arena. It is at the very centre of plant production and conservation, and all who use and enjoy plant products are stakeholders.

Chapter 5

Honey Bees: Biology and Status as Pollinators

Biology

Honey bees (*Apis mellifera*, family Apidae), a social species native to Europe, the Middle East, and Africa, are the most important pollinating bee in the temperate developed world (Fig. 5.1). They form large perennial colonies in hollow trees or other cavities, and they readily accept artificial hives. Man has cultured honey bees for thousands of years, and today's standard bee-keeping practices are familiar, predictable, and reasonably successful. There are 125,000–150,000 bee-keepers in the US who operate 3.2–3.4 million bee hives (Hoff and Willett, 1994) and about 35,000 bee-keepers in the UK who manage an estimated 200,000 colonies (Carreck and Williams, 1998). Altogether, there are an estimated 57.1 million hives of *A. mellifera* managed by bee-keepers around the world (Crane, 1990). Commercial bee-keepers provide honey, beeswax, other speciality hive products, bulk bees for sale to other bee-keepers, and pollination services.

In nature, honey bees nest in rock crevices, hollow trees, or other similar dry, hollow places. Worker bees secrete scales of beeswax from glands on the underside of their abdomens. They shape the wax scales into repeating, hexagonal cells that collectively make a comb. It is in these cells that food is stored and immature bees are reared. A natural bee nest contains up to ten or so combs.

The life cycle of a honey bee colony revolves around surviving winter or a similar dearth period and producing one or more new colonies early enough in spring to give the new colony time to collect food for next winter. Bees cluster together in a tight ball during winter to conserve heat, and the queen starts laying eggs in the centre of the nest in mid-winter when days start getting longer. Colony populations grow rapidly once natural *nectar flows* and *pollen flows* begin. By

Fig. 5.1. The honey bee, *Apis mellifera* L. (Source: Sadant and Sons.)

early spring, colonies are crowded with bees, and these congested colonies split and form new colonies by a process called *swarming*. A crowded colony rears several daughter queens, then the mother queen flies away from the colony accompanied by up to 60% of the workers. This *swarm* (Fig. 5.2) eventually occupies a new nest site, usually a hollow tree or wall void. Back at the original colony one of the daughter queens kills her rival sisters and inherits the colony. After the swarming season, the bees concentrate on storing honey and pollen for winter. By late summer, a colony has a central area full of brood and situated below layers of honey and pollen.

Because of this perennial life cycle a honey bee colony is potentially immortal, and nest sites tend to be occupied year after year. A colony occasionally may abandon a nest, a process called *absconding*, during a severe food dearth or if the colony is continually harassed by predators. However, even these abandoned nest sites are quickly reoccupied by new colonies because the odour of old nests attracts swarms.

Honey Bees as Pollinators

Honey bees are generalists that visit a wide assortment of blooming plants during a season. They are manageable, movable, well-known, and effective pollinators for many crops, hence they are the standard against which all other bee pollinators are measured. However, because they are generalists, honey bees are not the best pollinator for every crop. Unlike some solitary bees whose life cycles and behaviours are

Fig. 5.2. A honey bee swarm. Bees temporarily cluster on a branch or similar object before they relocate to a permanent nest site. (Source: Jim Strawser.)

perfectly matched for a particular crop, honey bees play the field for the richest reward. Thus, they are sometimes inefficient pollinators or easily lured away if competing flowers are more attractive than the crop of interest.

Honey bees can be practically bred for selected characteristics, including foraging behaviours. The availability of instrumental insemination brings this to a high degree of precision, but this technology is expensive and difficult to learn and not widely adopted by bee-keepers. It is possible to select for honey bees that preferentially collect a certain type of pollen, as shown in lucerne (Nye and Mackenson, 1968, 1970). However, bee hives used for pollination are normally cycled through many crops in one season, so it makes more sense to select for high pollen-hoarding strains rather than ones that prefer particular crops. Pollen foragers are generally more effective pollinators than nectar foragers (Vansell and Todd, 1946), probably because pollen foragers prefer inflorescences with relatively greater numbers of both male and female flowers (Gonzalez *et al.*, 1995). Fortunately, honey bees can be selected for high pollen-hoarding behaviour (Hellmich *et al.*, 1985; Gordon *et al.*, 1995).

Africanized Honey Bees and Pollination

All New World honey bees are descendants of honey bees brought to North and South America by settlers beginning in the 1600s. Bees imported from Europe flourished in temperate areas of the New World, and within three centuries there were large sustainable populations of European honey bees in North America and temperate South America. However, European bees did not thrive in tropical conditions, and to this day European honey bees do not prosper in South and Central America unless they are intensively managed by bee-keepers.

Researchers imported honey bees from Africa into Brazil in 1956 in an effort to improve bee-keeping in the New World tropics. These African bees were well suited to conditions in Brazil, and they began colonizing South America, hybridizing with European bees (a process called *Africanization*, resulting in *Africanized* honey bees), and displacing European bees. Compared to the relatively gentle European bees, Africanized honey bees are very defensive. Large numbers of them may sting people and livestock with little provocation. The bees began spreading northward, and today most of South America and all of Central America have established populations of Africanized honey bees.

The first naturally-arrived colony of Africanized bees in the US was found near Hidalgo, Texas in October 1990. By 1996 Africanized bees were present in parts of Texas, Arizona, New Mexico, California, Puerto Rico, and St Croix (Shimanuki, 1996). The ultimate range of Africanized bees and their hybrids in North America remains uncertain, but they will probably thrive best in semi-tropical latitudes. Their rate of spread seems to be declining (Shimanuki, 1996).

Africanized honey bees present many problems for commercial-scale crop pollination, and only a few benefits. We list here some of their documented liabilities relative to European honey bees:

- They frequently exhibit extreme defensive (stinging) behaviour. Colonies may stay defensive for several days after they are worked, thus endangering livestock, farm workers, and non-involved bystanders (Danka and Rinderer, 1986).
- Africanized colonies have smaller forager populations (Danka *et al.*, 1986b). Thus, on a per-colony basis, Africanized colonies field fewer potential pollinators.
- They do not retain large populations after being relocated. In Venezuela, 15 Africanized colonies and 15 European colonies were moved to six different crop sites over two months. Debilitating losses of adult bee populations were over twice as high in Africanized colonies (Danka *et al.*, 1987).

- Africanized bees forage more closely to their nests (Danka *et al.*, 1993a). Thus, Africanized colonies must be distributed nearer the target crop (increasing sting hazard for farm workers) and more uniformly throughout the crop (increasing handling costs).

There are some possible advantages of Africanized bees as pollinators relative to European bees:

- Africanized bees field a higher percentage of foragers (Danka and Rinderer, 1986).
- Flower handling time is equivalent, at least in cotton in southern Mexico (Loper and Danka, 1991). In other crops, they forage more rapidly which may improve the rate of pollen dispersal (Danka and Rinderer, 1986).
- Africanized bees are less susceptible to the commonly-used insecticides azinphosmethyl (Guthion®), methyl parathion, and permethrin (Ambush® or Pounce®) (Danka *et al.*, 1986a).
- Because they forage more closely to their hives, Africanized bees may be satisfactory pollinators in small restricted areas such as isolated fields used for growing hybrid seed (Danka *et al.*, 1993a).

Africanized bees are not a welcome addition to North American commercial crop pollination. Fortunately, the rate of Africanization slows when the bees move into areas with very large pre-existing populations of European bees. For example, by 1987 Africanized bees had reached the Yucatan peninsula of Mexico which contained a very large concentration of European bees. Extensive interbreeding between the two groups followed, resulting in bees with characteristics intermediate between African and European (Rinderer *et al.*, 1991). This *Europeanization* should continue as the bees move into heavily-European areas of the US.

However, Europeanization depends on large numbers of European bees. Wild honey bees are declining since the arrival of parasitic tracheal mites and varroa mites (see Chapter 4, page 24), and increasingly in North America the only available European bees are those maintained by bee-keepers. Thus, bee-keepers are the best defence North Americans have against Africanization. In the alarm that accompanies the arrival of Africanized bees, it is possible that citizens' groups or well-intentioned lawmakers may push to restrict bee-keeping in certain areas. Without European bee-keeping, the density of gentle European bees will decrease, leaving an area more vulnerable to Africanized bees. Only bee-keepers have the knowledge and resources to maintain the high densities of European bees necessary to limit the Africanization process locally.

Chapter 6

Honey Bees: Simplified Bee-keeping for Pollination

In some cases a grower may decide to buy and maintain honey bee colonies for the sole purpose of pollination. This chapter explains basic bee-keeping equipment, how to start colonies, and some minimum required management practices necessary to keep colonies strong and healthy for pollination.

A grower's first step is to determine the density of bee hives recommended for a particular crop (see Chapters 15–50) and then decide if keeping one's own bee hives is cost-effective. It is important to remember that the recommended density of bee hives is high for commercial plantings. But this need not be a serious deterrent. By housing bees in good equipment, treating bees for parasites, and feeding and medicating bees as needed, an average person can keep honey bees alive and reasonably productive with little other special attention. The concept of grower-owned honey bee colonies is not new. Commercial lowbush blueberry growers in Nova Scotia own and operate large apiaries to ensure good pollination.

Basic Hive Parts and Configuration

A honey bee *colony* is any single nest of bees containing combs, a queen, and a supporting population of workers; the term can apply to both wild and managed bee nests. A bee *hive* is a man-made structure that contains a colony of bees. In a standard Langstroth configuration, a bee hive is made up of stacked boxes called *supers*. Each super contains 8–10 removable combs (Fig. 6.1). Supers come in three common sizes – a deep super or *hive body* that is $9\frac{1}{2}$ in (24.1 cm) tall, a *medium super* that is $6\frac{5}{8}$ in (16.8 cm) tall, and a *shallow super* that is $5\frac{3}{4}$ in (14.6 cm) tall (Fig. 6.2). The heavy hive body (60+ lb when full of bees

Fig. 6.1. A deep Langstroth brood comb. (Source: Nancy B. Evelyn.)

and honey) promotes good production of *brood* (young developing bees), but the two smaller sizes are much easier for an average person to handle. Standardizing all supers to the medium size is a reasonable compromise between good brood production and bee-keeper convenience. A hive has a *bottom board* on which are placed the supers. It is

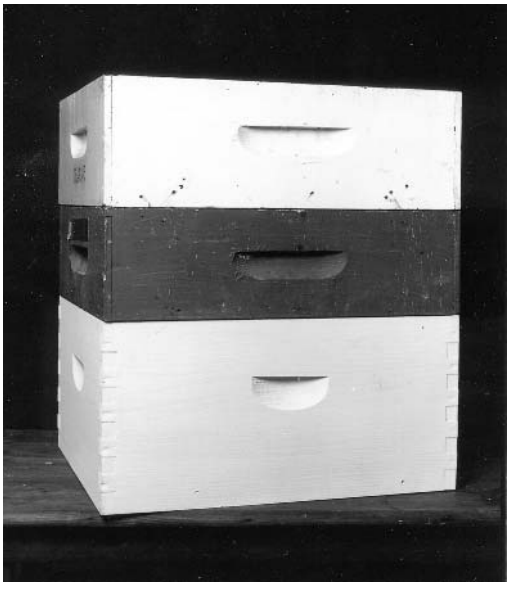


Fig. 6.2. Three common super sizes, deep (bottom), shallow (middle), and medium (top). (Source: Robert Newcomb.)

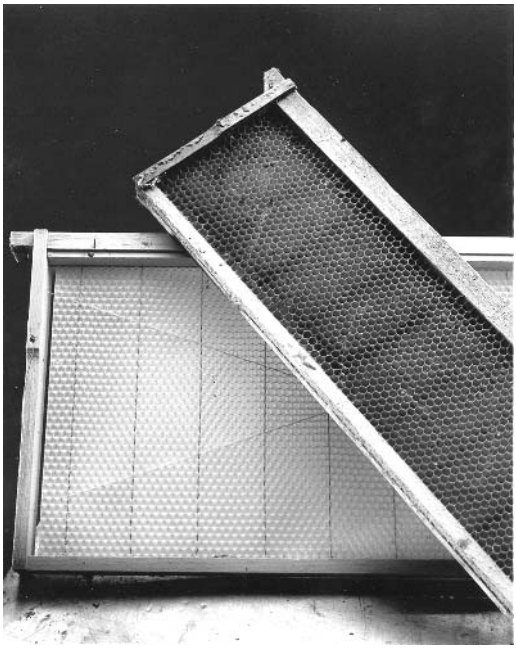


Fig. 6.3. The frame in the background is displaying a sheet of beeswax foundation. Bees 'draw out' the foundation with beeswax in order to make combs as seen in the foreground frame. (Source: Robert Newcomb.)

important to set the bottom board on concrete blocks or a similar type of waterproof stand in order to resist wood decay. Six or seven medium supers per hive should provide enough year-round space for bees, brood, honey, and pollen.

The combs inside supers are each made of a wooden frame in which is inserted *foundation*, a sheet of beeswax or plastic embossed with the shape of hexagonal cells (Fig. 6.3). Bees use foundation as a framework on which they construct their combs. The wooden frame makes the comb strong, movable, and interchangeable.

A lid goes on the top-most super. The simplest of these is a flat *migratory lid* with spacing cleats. These are inexpensive and practical if one plans to stack hives on top of each other during moves. The more durable choice is a combined *inner cover* and *telescoping outer cover*. The inner cover keeps bees from attaching comb to the outer cover and provides an insulating dead air space. The combined use of an inner and outer cover is especially suitable if one does not plan to move hives (Fig. 6.4). Appendix 1 presents a list of some well-known bee equipment suppliers.

Hive equipment within countries tends to be standardized and generally interchangeable. Hives are not inspected as intensely with

Fig. 6.4. The inner cover is resting on top of the hive body. Over the inner cover goes a telescoping outer cover. (Source: Nancy B. Evelyn.)

simplified bee-keeping for pollination as they are for honey production, and this justifies increased attention to good initial hive construction. In some countries it is common practice to first soak all wooden parts, except the comb frames, in copper-naphthenate wood preservative or in various mixtures of linseed oil and liquefied paraffin. These preservatives are relatively safe for bees and greatly increase the life of woodenware. Wood pressure-treated with copper chromium arsenate is not safe for bees. Once the wood preservative treatment has dried, one should assemble the exterior parts using wood glue in the joints and galvanized nails or wood screws as fasteners. By drilling pilot holes for nails or screws one can greatly reduce the chance of splitting wood. Finally, all exterior surfaces (but not the interior surfaces) should be covered with a good quality exterior-grade paint.

Other Required Bee-keeping Equipment

Other tools one will need to keep honey bees include:

- *Smoker* (Fig. 6.5): the most valuable tool for working bees. A smoker calms bees and reduces stinging behaviour. Pine straw, dry grass, and burlap make good smoker fuel.

Fig. 6.5. A bee smoker. (Source: Nancy B. Evelyn.)

- *Hive tool* (Fig. 6.6): ideally shaped for prying apart supers and frames.
- *Veil, gloves, and bee suit* (Fig. 6.7): protect body from stings.
- *Feeders*: hold sugar syrup that is fed to bees when natural food supplies become low. Several types of in-hive feeders are available in catalogues, but the most convenient and effective feeder is a clean, never-used paint can. These are available at paint stores. They are used by first punching one or two small nail holes in the lid, filling the can with syrup, capping it tightly, then setting it, hole-side down on top of the combs. The can is in turn covered with an empty super and lid.

Buying and Moving Colonies

The most simple, and sometimes economical, way to get started keeping bees is to buy established colonies from a reputable bee-keeper. It is advisable to arrange to inspect the colonies before buying and to ask

Fig. 6.6. A hive tool. (Source: Nancy B. Evelyn.)

Fig. 6.7. A complete bee suit affords the best protection against stings. (Source: Nancy B. Evelyn.)

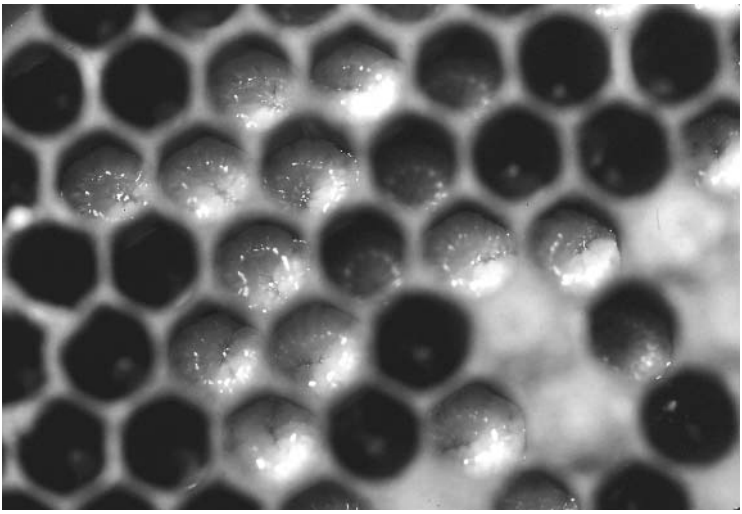


Fig. 6.8. Healthy young brood is glistening and pearly white. (Source: Keith S. Delaplane.)

the seller to provide a recent certificate of health inspection. Buying bee colonies can be intimidating to the uninitiated, and one way to boost one's confidence and gain a measure of protection is to invite a government bee inspector or trusted and qualified acquaintance to inspect the colonies and offer an expert opinion on the colonies' condition. It is important to buy bees that are housed in standard equipment and to reserve caution over bees that are housed in equipment that is shabby and deteriorated. The quality of the woodenware may be a good indicator of the quality of care the bees have received.

Once the colony is opened, the bees should be calm and numerous enough that they fill most of the spaces between combs. Each super should have at least nine frames of comb. If the adult bee population appears adequate, then it is time to inspect the brood. Capped brood is tan-brown in colour. Young, uncapped brood is glistening, pearly white (Fig. 6.8). A good-quality queen will have produced at least five or six combs of brood by mid-spring, and she lays eggs in a solid pattern so that there are few skipped cells.

If there is brood with perforated cappings, or if the larvae are tan, brown, or black, the colony may have American foulbrood disease. The deciding factor is the 'ropy test' which is done by taking a small stick or toothpick, inserting it in a suspicious cell of brood, mixing it up, and withdrawing it. If the brood is dead from American foulbrood disease it will be stringy and 'rope out' up to 1 inch (2.5 cm). This disease is very serious, very contagious to other colonies, and very difficult to control. It is also a reason to walk away from the potential purchase.

The parasitic mite *Varroa* sp. is a serious honey bee parasite in much of the developed world. Regular miticide treatments are now a normal fact of bee-keeping life, and bee-keepers who are negligent on this count will have relatively stressed and unhealthy colonies. It is a good idea to enquire of a seller's mite treatment regimen. In warmer latitudes the most recent miticide treatment should have been within the last 12 months. This interval may be longer in colder latitudes. Optimum mite treatment intervals vary considerably across regions, and this is a matter where an outside expert's opinion could be very useful.

Bee hives are easiest to move during winter when they weigh less and the bee populations are low. Moving hives requires at least two persons. It is best to move hives at night when all the bees are in the hive. Hive entrances are usually closed with a piece of folded window screen, and supers are fastened to each other and to the bottom board with a strap or hive staples. Hives are then lifted on to a truck bed or a trailer, then securely tied down with strapping or rope. It is important to remember to open hive entrances after the hives are relocated. If the temperature is very cold and bees are completely inactive there is no need to delay the move until night; however, extra care must be taken to avoid dropping or jostling hives in freezing temperatures because the cold, brittle combs may shatter and the bees may not be able to reform a tight cluster.

Fig. 6.9. A patty made of two parts powdered sugar and one part vegetable cooking oil helps protect bees from tracheal mites. (Source: Keith S. Delaplane.)

Installing Package Bees

Another way to start keeping bees is to buy package bees and install them in new hives. This method is more costly initially, but one has the assurance of healthy bees with a known history and the assurance of equipment built to one's own standards. Bees are routinely shipped in 2–5 lb (0.9–2.3 kg) packages of about 9000 to 22,000 bees. Detailed instructions for installing package bees are available from government extension services, bee supply companies (see Appendix 1), or various general texts (Graham, 1992; Morse, 1994; Delaplane, 1996).

Minimum Hive Management

Bee colonies used for pollination require a certain minimum amount of care, or they simply will not survive. If foulbrood and Nosema diseases are endemic in one's area, and if local regulations permit, one can treat bees with the antibiotic Terramycin® to prevent American and European foulbrood diseases and the antibiotic Fumidil® B to prevent and treat nosema disease. It is important to follow the manufacturer's label instructions explicitly with these and any other medications or miticides.

Beekeepers must monitor colonies closely to prevent starvation during times when nectar is not available. One can estimate a colony's weight relative to others in the apiary by hoisting each hive from the rear to get an idea of its weight. Colonies probably need supplemental feed if they weigh under 50 lb (22.7 kg). If autumn feeding is required it is best to feed a heavy syrup made of two parts sugar to one part water. In spring a lighter 1:1 syrup is preferable.

Protecting colonies from parasitic mites is one of the most crucial steps in bee-keeping, even in simplified bee-keeping for pollination. If tracheal mites are present at damaging levels in one's area, it is advisable to treat colonies with an approved miticide according to label instructions and according to the recommendation of local apiary health inspectors. A $\frac{1}{2}$ lb (227 g) patty made of two parts powdered sugar and one part vegetable cooking oil (Fig. 6.9) also helps control tracheal mites (Delaplane, 1992; Sammataro *et al.*, 1994). One way to check for varroa mites is to brush about 100 bees into a quart jar, spray them with ether-based automotive engine starting fluid, cap the jar, shake it, and examine the sides of the jar for mites. Mites are oval, brown, and a little larger than the head of a pin (Fig. 6.10). If varroa mites are present in one's apiary, the local apiary inspection officer or extension service are the best sources of control recommendations.

All bee hive medications and miticides are regulated by government agriculture or health agencies. It is important to check with one's

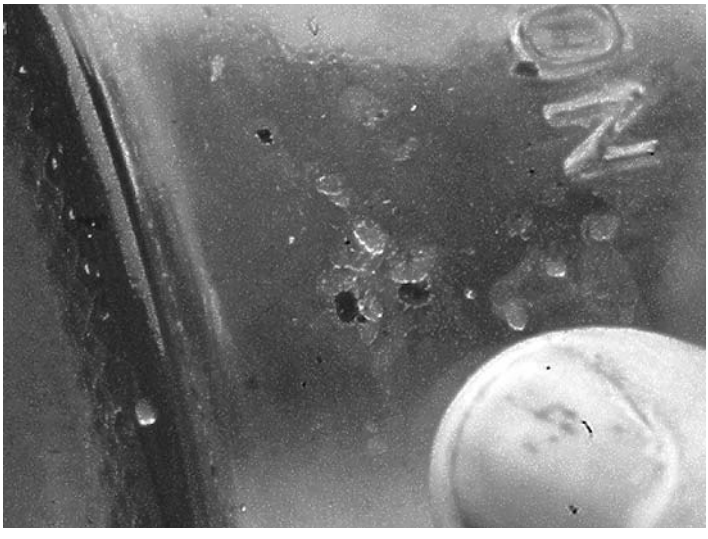


Fig. 6.10. Varroa mites show up against the side of the jar with an ether roll test. (Source: Robert Newcomb.)

extension service or government apiculturist to make sure whether a particular chemical is legal to use in one's area. Disease and pest control technology changes rapidly, and it is helpful to join a bee-keeping association or subscribe to at least one bee-keeping magazine or newsletter in order to stay abreast of the most current management recommendations.

Hive Placement and Timing

There is a benefit to be gained in using inexperienced bees for pollination, that is, bees that are not familiar with the area around the crop of interest (see Chapter 7, page 54). It is advisable for this reason to maintain bees at a location at least 2 miles (3.2 km) away from the crop of interest rather than maintain them at the crop site year-round. Bees should not be moved to the crop until it has begun some flowering. Once hives are sited, they should be orientated so that their fronts receive early morning sun. This stimulates early foraging which is important for pollinating many crops.

Chapter 7

Honey Bees: Managing Honey Bees for Pollination

Crop growers who need bee hives for pollination and the bee-keepers who rent them have different agendas. Growers want bees on the crop during the critical pollination window, but they also want them removed soon after bloom is finished so they will not interfere with other tasks. Beekeepers want income from colonies, but they also are concerned about sting liability, insecticide exposure, and keeping colonies strong for other uses. It is common for colonies to decline in strength while they are on crops that are poor sources of nectar and pollen. These motives underlie much of the negotiating when bee-keepers and growers are making pollination agreements. Education, understanding, good business standards, and the use of contracts can help bridge these differences.

A Good Pollinating Hive

Pollination brokers, grower associations, and government departments of agriculture have established and enforce minimum colony strength standards (Burgett *et al.*, 1984). This is a good practice that ensures growers of strong pollination units and establishes quality expectations and fee grades for bee-keepers.

It is normal for bee-keepers to add supers to hives to accommodate growing bee populations and honey stores. Thus, a very tall hive is probably strong. But it is possible for a rare unscrupulous bee-keeper to stack empty supers on weak hives to make them appear strong. A grower should not rely on external appearances. It is reasonable for the grower to ask the bee-keeper to open a few hives for random inspection, but the grower must know what to look for. When the hive lid is removed, bees should immediately 'boil over' and blanket the

Fig. 7.1. In a strong colony the bees will blanket the tops of six to ten frames. (Source: Jim Strawser.)

tops of six to ten frames (Fig. 7.1). Bees do not well up so dramatically in colonies with small populations (Fig. 7.2). There should be enough adult bees to fully cover six to ten combs. Four to six of those combs should be well filled with brood. When brood is young, it is possible to see glistening white larvae in their cells, but older brood are covered with cardboard-coloured wax cappings. Bees are best motivated to collect pollen, and hence are more efficient pollinators, when they have young, uncapped brood. A colony in two hive bodies usually meets these minimum strength criteria. Single-storey hives can make good pollinating units, but with singles it is important to make sure they have enough bees and brood. Very strong colonies are superior pollinators, and the bee-keepers who provide them should get premium rental fees.

Some bee-keepers specialize in producing package bees for sale to other bee-keepers. These bee-keepers also may rent hives for pollination, and they may want to harvest bees from their on-site pollination hives to make up package bee orders. This does not necessarily diminish the value of colonies for pollination if the bee-keeper does not remove queens nor remove so many workers that the colony is seriously weakened. In fact, harvesting bees for packages stimulates brood production as the colony tries to compensate for lost population, and high levels of brood rearing generally improve pollination efficiency.

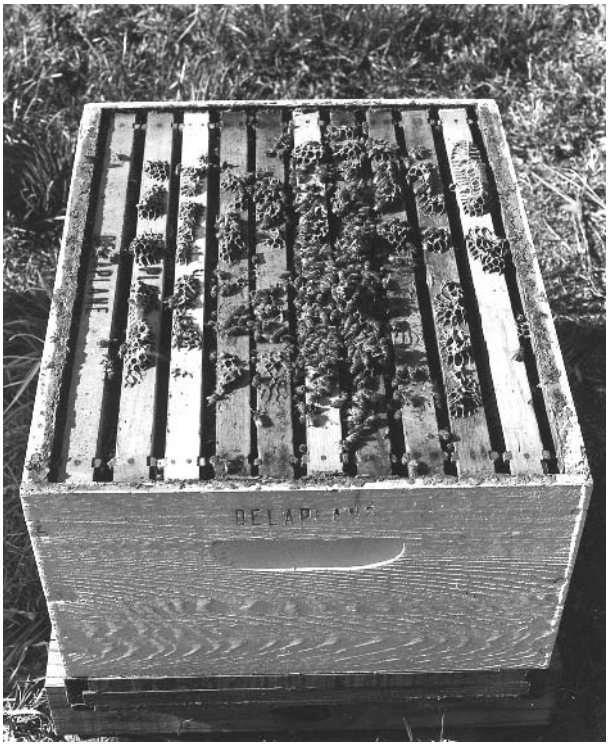


Fig. 7.2. A comparatively weaker colony. (Source: Jim Strawser.)

Moreover, harvesting bees also discourages swarming. Colonies that are overpopulated are prone to swarm, and swarming severely weakens colonies for pollination purposes. Colonies that swarm endure a period of broodlessness for several days or even weeks as the colony rears a new queen, she mates, and begins laying eggs. It is much better to use pollination colonies simultaneously for package bee production than to let them swarm. Of course, from the grower's perspective it is best if colonies are (i) not used for package production and (ii) do not swarm, but other swarm-prevention measures are labour intensive. These matters can be negotiated in pollination contracts.

Moving Hives

Bee hives are often moved at night when the bees are not flying and temperatures are cooler. Some bee-keepers may screen hive entrances individually and manually load hives on and off a truck. Other bee-keepers group hives, usually four to a pallet, and load them with a forklift on to a trailer or flatbed truck; in these cases, the bee-keeper

may net the entire truckload to contain flying bees. In either case, the grower should be prepared for night-time arrival and arrange details in advance with the bee-keeper about field access and hive placement.

Timing

It is best to use honey bees that are inexperienced at foraging in the area near the crop of interest. That way, upon delivery to the orchard the bees will immediately begin working on the crop because they have not yet discovered other more attractive plants blooming in the area. There are exceptions to this recommendation, namely with almond (see Chapter 16, page 141) and cranberry (see Chapter 36, page 222).

To gain the benefit of inexperienced bees, it is necessary to move hives into the crop after it has already begun flowering a little. If the colonies arrive before the crop starts blooming there is a strong likelihood that the bees will learn to forage on non-target plants such as dandelion. Once bees are trained to such competing flowers, they may ignore the crop when it blooms. Chapters 15–50 have information on timing recommendations for specific crops.

Irrigation and Bee Activity

Overhead irrigation decreases the bee foraging rate for nectar and, possibly, for pollen (Teuber and Thorp, 1987). Open flower designs, like those found in melons and cucumbers, can fill up with water and lose their attractiveness to bees. As much as possible, growers should avoid irrigating during bloom times and during daylight hours when bees are pollinating.

Recommended Bee Densities

The recommended hive density depends on the attractiveness of the crop, the population density of non-managed bees, the abundance of competing natural nectar sources, strength and location of bee hives, weather, and the grower's experience. The goal is to use the minimum hive density that provides a maximum crop yield. Generally, any existing factor that reduces overall pollination efficiency (unattractive crop, few non-managed bees, many competing nectar sources, poor weather, etc.) calls for an increased rate of imported pollinators to compensate for the natural deficiency. A grower can generally consider one hive per acre (2.5 ha^{-1}) as a starting point in the decision

making process, then use more or less according to the advice of crop consultants or extension specialists. Chapters 15–50 provide recommended bee densities for specific crops.

Hive Placement

It is in the grower's best interest to have hives as close as possible to the crop of interest. The number of bees visiting the crop, amount of pollen collected, and crop yields generally increase the closer the hives are to the crop (Bohart, 1957; Peterson *et al.*, 1960; Alpatov, 1984).

It is helpful to orientate hives so that they are exposed to early morning sun. This stimulates bees to visit flowers early, and pollination early in the day is important in many crops. Hives should be placed on knolls or high ground, and never in low areas which are prone to accumulate cool, damp air. Bees in chilly, shaded conditions are comparatively more reluctant to fly. Hives should be protected from strong winds with bales of straw, hedges, or similar types of wind barriers. As much as possible, hives should be located away from farm workers, pedestrians, and livestock. Likewise, hives should not be placed near dwellings nor irrigation valves. It is important that the bees have a source of water, especially during summer drought

Fig. 7.3. A saturation situation in which hives are grouped within the field at 500 ft (153 m) intervals so that their 300 ft (92 m) optimum foraging radii overlap. (Source: Carol Ness.)

conditions. The bee-keeper can provide this by placing near the hives open containers of water with floating wood or polystyrene chips. The floating objects help prevent bees from drowning.

Honey bees prefer to work within 300 ft (92 m) of their colony, although they can fly several miles if necessary. For this reason, by putting groups of hives at 500-ft (153 m) intervals (about 0.1 mile) throughout a field, one can place a whole field within ordinary bee foraging range (Levin, 1986) (Fig. 7.3); however, this is not always practical. If the interior of a field is inaccessible, one can group hives around the edges. In these cases, the centre of the field is less likely to be visited by bees, but the bee-keeper can offset this problem by putting more colonies in the centre-most groups along the field edge; this increases competition and forces bees to forage deeper into the field (Levin, 1986) (Fig. 7.4).

Hive dispersal can be a point of difference between growers and bee-keepers. For the bee-keeper, dispersing hives throughout a field is labour-intensive, but it is desirable for the grower to have well-dispersed hives. It is likely that a hive's microclimate is more important than its location in the field. It is better to locate hives in sunny, wind-protected sites along field edges than in low, cool spots in field interiors. The degree of hive dispersal, and who will do it, should be clearly worked out in a contract (see Appendix 2) with the rental fee adjusted accordingly. Sometimes bee-keepers simply deliver hives at a central location and it is the growers who distribute them with their own equipment.

Fig. 7.4. A grower can use competition to encourage bees to forage more deeply into inaccessible field interiors. Bees from a large number of colonies grouped together (centre) will forage further from their hives and penetrate more deeply into a field interior than will bees from isolated colonies (left and right). (Source: Carol Ness.)

Non-Crop, or 'Competing' Bloom

The idea of removing wild plants whose bloom coincides with the crop is controversial. In one study, honey bees ignored apple blossoms and instead concentrated on dandelion that was growing in the same orchard (Mayer and Lunden, 1991). Removing competing bloom (by mowing or herbicides) can improve crop yield in some situations. Bee activity in lucerne and subsequent seed set were higher after nearby flowering mustard was mowed (Linsley and McSwain, 1947). However, an abundance of flowering plants can also attract foraging bees to an area, encourage non-honey bees to nest near the crop, and improve the reproductive output of bumble bee colonies (see Chapter 4). Recent thinking is clearly in favour of enhancing, not eliminating, bee pasture in the interest of building up diverse populations of pollinators. Synthetic honey bee attractants may help when competing bloom is a problem (see page 58).

Pollen Dispensers or Inserts

Pollen dispensers are devices that fit at the entrance of bee hives and hold pollen of desirable pollenizer varieties in such a way that the bees dust themselves with the pollen as they leave the hive. Dispensers possibly stimulate bees to forage for the pollen type in the insert (Lötter, 1960) which, if true, would certainly be an argument in their favour. Plus, inserts may be an attractive option with old solid-block orchards that have no pollenizers planted nearby (Anonymous, 1983; Mayer and Johansen, 1988). However, the overall value of pollen dispensers in increasing yield is doubtful (Jay, 1986).

Bees inadvertently dust each other with pollen inside the hive. Consequently, departing foragers carry a variety of pollen grains on their bodies, not all of which is from the plant species they are currently working (DeGrandi-Hoffman *et al.*, 1984). In one study, newly-emerged bees that had never flown had collected enough 'second-hand' pollen on their bodies within 3–4 h in the hive that researchers could successfully hand-pollinate apple flowers with the bees' bodies (DeGrandi-Hoffman *et al.*, 1986). Clearly then, this in-hive exchange of pollen is beneficial. Free *et al.* (1991) installed 'two strips of clean nylon bristles' (either 0.18 mm or 0.07 mm diameter) at the entrance of bee hives so that bees entering and leaving the hive had to brush against them. The objective was to increase further the exchange of pollen by bees at the hive. The entrance bristles generally increased the number and species diversity of pollen grains on departing foragers. Since pollen quickly loses its viability inside a hive (Kraai, 1962), Free and his co-workers argued that pollen exchanged at

the hive entrance may be more viable. Entrance bristles are inexpensive and easy to use, but research is needed to see if they significantly improve crop pollination.

Hive inserts may also have promise for spreading biological pest control agents in crops. Dispenser pollen in one study was treated with bacteria that are antagonistic to the fireblight disease organism in apple and pear. Bees picked up the favourable bacteria on their bodies and delivered them directly to apple and pear flowers, the site of the disease (Thomson *et al.*, 1992). Gross *et al.* (1994) successfully used honey bees and a similar entrance insert to spread a beneficial virus to control defoliating caterpillars in clover.

Pollen Traps

Pollen traps are devices attached to the entrances of bee hives that are used to harvest pollen loads off foraging bees. It has been thought that pollen traps may induce a pollen deficit in the colony, thus increasing the proportion of bees foraging for pollen and thereby increasing the effectiveness of the colony as a pollination unit. Webster *et al.* (1985) tested this hypothesis with honey bee colonies in almond and plum orchards and determined that colonies with traps had higher proportions of foraging bees with pollen loads than did colonies without traps. This potential benefit was partly offset by a decrease in brood production in colonies continuously fitted with traps, but pollen traps have been shown in other situations not to decrease brood production (Goodman, 1974; McLellan, 1974).

Honey Bee Attractants

Honey bee attractants are products designed to increase bee visitation to treated crops with the goal of increasing pollination, fruit-set, yield, and ultimately profits. These products are mixed with water and applied to crops with conventional spray equipment.

Several attractants have been marketed, and most have had a doubtful performance record. However, the situation may be improving with recent advances in our understanding of *pheromones* – 'external hormones' that insects secrete to regulate the behaviour and physiology of other individual insects. Honey bees have a rich battery of pheromones. Synthesizing and manipulating these chemicals may give bee-keepers and crop growers important new tools for pollination.

In general, attractants are warranted only when conditions are suboptimal for pollination or when the crop is not attractive to bees. The idea is to focus bees away from competing bloom, improve their

efficiency when foraging conditions are poor, or to improve their efficiency when their numbers are low relative to the amount of bloom needing pollination. Some situations in which an attractant may be advisable are:

- A grower may apply attractant to the centre of a large field to increase bee visitation there if the bee-keeper was able to locate hives only on the periphery.
- An attractant may increase bee visitation in crops such as cranberry and pear that are known to be comparatively unattractive to bees.
- Attractant may help keep bees foraging in crops during times when natural nectar flows would otherwise lure them away. Most honey producers are aware of the natural nectar flows in their area. In a good working relationship, a bee-keeper can alert his client grower of the risk of competing plants and advise the use of an attractant.
- Attractant may be advisable when cool weather is discouraging bees from flying or when a late-season freeze has decreased the number of viable flowers.
- Attractant may help focus pollinators on the crop if a sudden period of warm weather has compressed bloom and the resulting number of flowers requiring pollination is nearly too much for the available bees.

Bee attractants encourage bee *visitation*, not necessarily bee pollination. If the flowers are not appealing to bees, no chemical attractant will make bees work them. Likewise, if there are no bees in the area, an attractant will not draw them in from great distances. A grower's first priority must be the bees themselves.

Some products have been marketed which contain sugars, attractive oils, or some components of *Nasonov* pheromone, a pheromone that bees use to orientate to nest sites and to low-odour resources such as water. Some trade names are Bee-Here®, Beeline®, Beelure®, Bee-Scent®, and Pollenaid®. The research support for these products is generally not strong, but more work is certainly warranted (Winston and Slessor, 1993). Sugar-based attractants are shown to actually diminish pollination efficiency because bees are diverted to collecting syrup off foliage instead of pollinating the flowers (Free, 1965). Beelure®, a sugar-based product, does not increase bee visitation to apple blossoms (Rajotte and Fell, 1982). Clearly, future research should focus on pheromone-based products.

In a study by Mayer *et al.* (1989a) in Washington state, Bee-Scent®, a Nasonov pheromone-based attractant, increased honey bee visitation for 24 h post-treatment in 'Red Delicious' apple, 'Van' cherry, pear ('Bartlett' and 'Bosc'), and 'President' plum. It did not increase visitation in 'Anjou' pear. In some orchards, bee visitation was elevated for

72 h post-treatment. Bee-Scent® increased fruit-set by at least 23% in 'Bartlett' pear, by 44% in 'Anjou' pear, by 12% in 'Van' cherry, and by 5–22% in 'Red Delicious' apple. Bee-Scent Plus® increased fruit-set by 44% in 'Bartlett' pear, by 15% in 'Van' cherry, by 88% in 'President' plum, and by 6% in 'Red Delicious' apple. Mayer and his co-workers did not measure orchard yields.

Bee-Scent® increased honey bee visitation in Arizona watermelon for up to two days in a seedless variety and in the variety 'Picnic,' but it did not increase yield in either variety (Loper and Roselle, 1991). Bee-Scent® did not improve bee visitation, yield, or monetary return with the watermelon variety 'Royal Sweet' nor cucumber variety 'Calypso' in North Carolina (Schultheis *et al.*, 1994).

Bee-Scent® increased bee visitation in 'Stayman' and 'Triple Red' apple and increased fruit-set in 'Stayman' and 'Yellow Delicious' in Virginia (R.D. Fell, unpublished report).

Beeline®, a bee food supplement spray, may increase yield in cucumber (Margalith *et al.*, 1984), but it does not increase bee visitation nor yield in carrot seed (Belletti and Zani, 1981) nor in red clover (Burgett and Fisher, 1979). Beeline® did not improve bee visitation, yield, or monetary return in 'Royal Sweet' watermelon in North Carolina (Schultheis *et al.*, 1994).

The most promising and recent development with bee attractants has focused on synthetic honey bee *queen mandibular pheromone* (QMP). Although the existence of QMP was known since the 1960s (Callow and Johnston, 1960; Butler and Fairey, 1964), all of its components were not characterized until nearly 30 years later (Slessor *et al.*, 1988, 1990; Kaminski *et al.*, 1990). Researchers and industry have since synthesized and developed QMP into commercialized products.

In nature, QMP is the key pheromone that informs bees of the presence of a queen. QMP stimulates worker bees to form a 'court' or retinue around the queen. As bees lick and groom the queen, they pick up QMP in the process. These bees then act as messengers, spreading the pheromone from bee to bee, providing a calming, stabilizing effect. Among other things, the presence of a queen (i.e. her pheromones) stimulates worker bees to live longer (Delaplane and Harbo, 1987) and possibly forage more. At least one product with synthetic QMP (Fruit Boost®) is now marketed as a bee attractant for enhancing crop pollination. QMP works as a pollination aid by stimulating greater bee recruitment to treated plots and by stimulating individual foragers to stay in treated plots longer and visit more flowers (Higo *et al.*, 1995).

QMP-based bee attractants increased honey bee visitation in pear varieties 'Anjou' and 'Bartlett' in Washington and British Columbia. QMP-based attractant increased bee visitation in 'Red Delicious' apples in British Columbia, but it did not affect yield nor fruit quality

(weight and diameter). However, the attractant increased fruit diameter in pear which translated to a US$427 acre^{-1} (US$1055 ha^{-1}) increase in farmgate revenue (Currie *et al.*, 1992b). In a later study, QMP-based attractant increased fruit size in 'Anjou' pear by 7% which translated to a US$162 acre^{-1} (US$400 ha^{-1}) increase in farmgate revenue; however, the attractant did not increase bee visits, fruit-set, nor fruit size in 'Bing' sweet cherry (Naumann *et al.*, 1994b).

QMP-based attractant increased bee visitation in cranberry varieties 'Crowley' and 'Stevens' and in the highbush blueberry 'Bluecrop' (Currie *et al.*, 1992a). Maximum attractiveness to bees was achieved in cranberry with a concentration about ten times less than that for blueberry or for the apple and pear data cited by Currie *et al.* (1992b). This suggests that more attractant is needed for a three-dimensional surface (i.e. bush or tree crops) than for a flat surface (i.e. a cranberry bog). Bee flight conditions were poor in the first year of the cranberry study and the attractant increased yield 41% and farmgate revenue by US$3564 acre^{-1} (US$8804 ha^{-1}). In the second year, weather conditions for pollination were excellent and the attractant did not improve yield nor revenue. In two out of 3 years of highbush blueberry trials (Currie *et al.*, 1992a), QMP attractant increased fruit yield by at least 6% and farmgate revenue an average of US$364 acre^{-1} (US$900 ha^{-1}).

In New Zealand, QMP-based attractant increased kiwifruit yield (trays harvested per ha) by 24%, and tended to increase export fruit weight (M. Partridge, Phero Tech Inc., unpublished data).

Disposable Pollination Units

Disposable pollination units (DPUs) are small colonies housed in inexpensive containers and whose sole purpose is pollination. They are destroyed or left to die after flowering is finished. DPUs can be started from conventional package colonies. DPUs may be attractive for growers with remote orchards or for bee-keepers who have surplus bees. However, DPUs have not been widely adopted.

One study compared foraging performance of bees in traditional overwintered colonies or in DPUs made of modified polystyrene foam coolers with free or caged queens and 3 or 6 lb (1.4 or 2.7 kg) of bees. Flight activity and pollen storage were generally higher in traditional overwintered colonies, but performance of DPUs was much more uniform (Thorp *et al.*, 1973). This was the case even when researchers intentionally chose uniform overwintered colonies. In another study, overwintered colonies had a higher percentage of pollen foragers and a higher percentage of total foragers (Erickson *et al.*, 1975). Bees from DPUs effectively set fruit, at least in almond, but researchers recommend that growers use twice as many DPUs as conventional bee hives

(Erickson *et al.*, 1977). Shipping DPUs in the mail has not been successful (Thorp *et al.*, 1973).

Foraging activity of polystyrene DPUs and conventional colonies was compared on apple varieties 'Delicious', 'Jonathan', 'Red Delicious', and 'Yellow Delicious' in Maryland. Conventional colonies began to forage earlier in the day, but DPUs worked longer in the afternoon. The percentage of pollen foragers did not differ (Tew and Caron, 1988a). In cucumbers, the researchers compared the performance of DPUs, conventional colonies with abundant space, and conventional colonies that were crowded for space. The number of pollen foragers was highest in conventional colonies with abundant space and lowest in conventional colonies that were crowded; DPUs were intermediate (Tew and Caron, 1988b).

Queenless DPUs are inexpensive to set up, and they dwindle rapidly after the flowering season ends. However, bees from queenless DPUs are comparatively inefficient foragers (Kauffeld *et al.*, 1970). One solution to this problem may be synthetic QMP. Queenless workers treated with QMP forage normally, and the colony does not reproduce. Queenless DPUs with QMP were compared to queenless DPUs without QMP and to DPUs with live queens (Currie *et al.*, 1995). Compared to queenless DPUs without QMP, the number of foragers tended to be higher in DPUs with either a queen or QMP; however, the results were not always significantly different. In another study, bees from queenless DPUs treated with extracts of queens foraged on glasshouse cucumber similarly to DPUs with live queens (Krieg, 1994). One product with QMP is marketed under the trade name Bee Boost®, and one of the advertised uses is to 'stabilize disposable pollination units'. If non-reproducing queenless QMP-treated units could be made of biodegradable materials, there would be no need to revisit the DPUs after they are set out.

In general, DPUs have not been widely adopted and, so far, are not cost-effective. However, their uniformity of performance and portability make them a promising avenue for additional research. Improvements in pheromone technology and mail transit may make them more feasible.

Chapter 8

Bumble Bees

Biology

Bumble bees (*Bombus* spp., family Apidae) are large, hairy bees whose species are concentrated in the temperate regions of the world. Like honey bees, they were intentionally exported outside of their native ranges into other countries including Australia, New Zealand, the Philippines, and South Africa. There are about 400 species worldwide (Heinrich, 1979) and at least 54 species in North and Central America (Michener *et al.*, 1994).

Bumble bees are social bees with an annual colony life cycle. They first pass through a solitary phase (as single queens) before reproducing into a colony of numerous, social individuals. This is contrasted with the perennial honey bee colonies that never have a solitary phase.

The bumble bee life cycle begins with a young, mated queen that overwinters in isolation in some dry, safe harbourage in the ground or under loose tree bark. In spring she becomes active, foraging for early nectar and pollen with which she builds up energy reserves for brood production. She seeks out a nest site in such places as grass thatch, piles of hay, or abandoned rodent nests. She must choose a dry, well-drained site that will be safe from flooding.

The queen builds a thimble-shaped beeswax *honeypot* in which she stores nectar. Nearby she forms a lump of field-collected pollen, excavates a depression in it, and lays one or more eggs in the depression, covering it with wax. The eggs hatch and the young larvae feed on their bed of pollen, and as they grow the queen opens the wax covering and adds more pollen and nectar. When she is not foraging, the queen perches on this *brood clump*, incubating the larvae to speed their development. As the larvae mature, each spins a cocoon of silk in which it pupates and completes development into an adult. After new workers emerge, their empty cocoons are used as storage pots for honey

Fig. 8.1. A male bumble bee, *Bombus impatiens*. (Source: Keith S. Delaplane.)

or pollen. More pollen lumps with eggs are deposited alongside or on top of the old ones, and thus the irregular comb grows. Eventually, there are enough workers to do the foraging and housekeeping tasks so that the queen can concentrate on laying eggs. Colony population peaks at a few hundred individuals (Sladen, 1912; Heinrich, 1979).

The colony switches from producing workers to producing males (Fig. 8.1) and new queens (Fig. 8.2) some time in mid- to late summer. Males leave the nest a few days after emerging. The new queens linger in the nest a while longer, eating food collected by workers, foraging for their own food, and occasionally foraging for the colony. The new queens mate and seek out a suitable overwintering site. Males, workers, and the old queen die before winter.

The entire season's activities – nest founding, worker production, and food collection – are all aimed at producing next year's queens in mid- to late summer. A colony's success at queen production depends largely on the abundance of flowers in its habitat (Bowers, 1986), although other factors such as parasite intensity (Schmid-Hempel and Durrer, 1991) play a role. A prolonged shortage of flowers, which is common during mid-summer in some areas, can severely reduce queen production. Mortality of young queens is high. Of the hundred or so queens that one colony produces, on average only one survives to produce another generation of queens (Heinrich, 1979). Bumble bees are attacked by parasites, vertebrate predators, and 'cuckoo' bees (*Psithyrus* spp.) that take over bumble bee nests through social parasitism.

Bumble Bees as Pollinators

Like honey bees, bumble bees are generalists and visit a wide assortment of flowering plants. However, because of their different morphology and behaviours bumble bees may be superior pollinators for certain crops, especially in glasshouses.

Among bees as a whole, honey bees are comparatively short-tongued and bumble bees are long-tongued. This gives bumble bees the advantage in pollinating flowers with deep tubular corollae such as broad bean and red clover. The value of bumble bees as pollinators of red clover has long been recognized and was the impetus for importing these bees into New Zealand in the 19th century. Species of bumble bees vary in tongue length, and they generally segregate themselves among crops so that longer-tongued species predominate at crops with longer corollae and vice versa (Ranta and Tiainen, 1982; Fairey *et al.*, 1992; Plowright and Plowright, 1997).

Bumble bees are large, and this may increase their chances of contacting the sexual parts of a flower and enable them to carry larger pollen loads than do other bees. This may explain why bumble bees pollinate male-sterile cotton in cage tests more efficiently than honey bees (Berger *et al.*, 1988). It also may explain why bumble bees increase fruit-set in cucumbers more effectively than honey bees when compared at an equal number of bee visits (Stanghellini *et al.*, 1997).

Some flower designs impede good pollination by honey bees, but are no problem for bumble bees. For example, lucerne flowers must be

Fig. 8.2. A female queen bumble bee, *Bombus impatiens*. (Source: Keith S. Delaplane.)

'tripped' to expose the sexual parts to a visiting insect. Bees automatically trip the flower with their body weight as they enter it from the front, causing the pistil and anthers to snap up and strike the bee on the head. Often, honey bees endure this only once and thereafter avoid a blow by *robbing* the flowers – that is, by probing them for nectar from the side and completely bypassing the sexual parts (Heinrich, 1979). Bumble bees and other non-honey bees, on the other hand, do not seem to object to this insult from the flower, and keep foraging on lucerne legitimately. Other types of flowers release pollen only when the flower is sonicated, or buzz-pollinated (see Chapter 3, page 20). Bumble bees and certain solitary bees are capable of doing this, and this makes them valuable pollinators of buzz-pollinated crops such as blueberry, eggplant, seed potato, and tomato (Plowright and Laverty, 1987; Cane and Payne, 1990).

Bumble bees, compared to other bees, are more tolerant of inclement weather. They often forage even during rain or strong wind. Bumble bees generally commence foraging at cooler temperatures than do honey bees (Corbet *et al.*, 1993).

Bumble bees have a good record as pollinators in glasshouses. They do not fly against windows like honey bees, and they are less likely to forage outside the glasshouse when windows must be opened for temperature control. Honey bees have been known to spot with their faeces the surfaces of a glasshouse to the extent that it restricts sunlight and plant productivity.

Bumble bee foragers are incapable of recruiting each other to food resources as do the honey bees (Heinrich, 1979). This means that an individual bumble bee is less likely to be diverted away from the crop to a more rewarding competing bloom. However, this hypothesis warrants more testing. Bumble bee individuals make foraging decisions based on reward, and these individual decisions would add up to colony-level efforts. Thus, one could expect a bumble bee colony to eventually orientate to the richest resource even if it took longer to do so than a honey bee colony.

Compared to honey bees, when foraging in raspberry bumble bees visit a higher proportion of pollen-bearing flowers, visit flowers earlier in the morning when pollen is most abundant, visit more flowers per minute, carry more pollen on their bodies, and deposit more pollen on raspberry stigmas (Willmer *et al.*, 1994). In cranberry, bumble bees have purer loads of cranberry pollen and visit more flowers per minute than do honey bees (MacKenzie, 1994).

The usefulness of bumble bees as pollinators is limited by their annual life cycle, small colony populations, and small scale of domestication. For example, only bumble bee queens, not full-size colonies, are present in time for early-blooming blueberry. Thus, the number of available foragers at that time of year is lower than the species' poten-

tial. This problem could be mitigated if bee-keepers could induce bumble bee queens to nest prematurely in order to achieve full-size colonies in time for early-blooming crops. This technology is being developed by a few companies in Europe and North America which are selling bumble bee colonies for pollination, mostly for glasshouse crops. Methods for large-scale bumble bee-keeping are proprietary secrets, but the fundamentals are known and published (see page 71).

Conserving Wild Bumble Bees

Chapter 4 covers bee conservation in detail. However, for wild bumble bees there are two principles that warrant repeating here. First, bumble bees nest in grassy thatch and abandoned rodent nests. One can conserve nesting sites by simply leaving unmown the grassy margins around fields and orchards. It is important that these areas are never disturbed by heavy machinery compaction, herbicides, insecticides, or ploughing. Second, of all the non-honey bees, bumble bees are the most dependent on a season-long succession of blooming plants. Production of queens and males in mid- to late summer depends largely on the quantity of food plants available in the preceding weeks. A mid-summer dearth can reduce a colony's output of reproductives. One way to provide an unbroken succession of bloom is to install bee pasture, preferably with perennial plants. It was found in south Georgia, USA blueberry orchards that althea (*Hibiscus syriacus*), abelia (*Abelia* x *grandifolia*), vitex (*Vitex agnuscastus*), red clover (*Trifolium pratense perenne*), Mexican heather (*Cuphea hyssopifolia*), monkey grass (*Liriope muscari*), summer sweet (*Clethra alnifolia*), and giant sunflower (*Helianthus giganteus*) are promising candidate plants for supplemental bumble bee pasture (Krewer *et al.*, 1996).

Rearing Bumble Bees

There are three approaches to producing hived bumble bees for use in pollination: (i) hiving natural colonies collected from the field; (ii) setting out artificial nest boxes to attract wild queens; and (iii) inducing bumble bees to nest year-round in captivity. The first two approaches appear simple but they give the grower minimum control over colony growth or synchrony with crop bloom; moreover, their success rate is poor. The third approach is labour intensive but lets one produce full-size bumble bee colonies at any time of the year; it represents the complete domestication of the bumble bee. Rearing bumble bees is labour intensive and fraught with variability. Nevertheless, a core of knowledge exists and the field is ripe for development.

Hiving colonies from the field

Bumble bee nests are not easy to find because they are usually located underground or in thick thatch. But if a natural colony is located it is possible to hive it using a few simple tools including a bee veil (see Appendix 1), gloves, a sheer insect-collecting net, one or more quart jars with lids, shovel, and some kind of hive for the colony. Any kind of weather-resistant box with a removable lid and small entrance hole can serve as a hive. The hive's entrance must be temporarily closed with window screen or fine hardware cloth.

After one has donned protective clothing and before the nest is exposed it is possible to catch a large number of bees with a net as they fly to and from the entrance. Bees can be transferred from the net to a quart jar by scooping bees up in the jar as they walk up the sides of a net that has been inverted so that the opening faces down. After a while one can then begin excavating the nest, catching bees along the way. For nests near the surface, it is relatively easy to pull aside grass to expose the comb, carefully pick up the comb, and put it in the hive. A shovel will be necessary for underground nests. Most bees have usually been caught by the time the comb is reached. After the comb has been transferred to the hive and all the bees are in the jar, the bees can be rapidly shaken into the hive and the lid quickly closed. The new hive should be relocated at least $\frac{1}{2}$ mile (0.8 km) away to discourage foragers from flying back to their original nest site. The temporary closure across the entrance can then be removed.

An alternative method is to transfer the comb and bees at night with the help of a red light (bees do not see red well). That way, one can capture more of the workers since most of them will be home for the night. They are also less likely to fly in the dark.

Relocated bumble bee colonies are stressed and one way to help them survive the ordeal is to temporarily provide them with food. They can be fed sugar syrup (1 part sugar:1 part water) or diluted honey in a gravity feeder that is inserted through the wall of the hive.

Berger *et al.* (1988) transferred field-caught and hived bumble bee nests to a field of male-sterile and male-fertile cotton in Texas. They set out eight nests at ~50-ft (15 m) intervals along the 12 acre (5 ha) field. All colonies survived the transfer, resumed foraging, and continued rearing brood. Although only eight bumble bees were seen foraging on the cotton in 4 weeks of observation, up to 21% of the pollen reserves in the nests was cotton pollen. All colonies were parasitized with cuckoo bees by late August which seriously reduced the likelihood of the bumble bee colonies producing queens for the next season.

Fig. 8.3. An above-ground artificial bumble bee nest box after the design of Hobbs *et al.* (1960) and Hobbs (1967). The box is attached to the ground with a loop of heavy wire running through two eyelets and into the ground. (Source: Keith S. Delaplane.)

Providing artificial nesting sites

The rationale for using artificial nest boxes is to increase local bumble bee populations by providing adequate nesting sites. This presupposes that nesting sites are a limiting factor in the local habitat. Queens become active and start seeking nest sites on warm days in spring when the first pollen sources begin to bloom. This is the time to set out artificial nest boxes.

Hobbs *et al.* (1960) and Hobbs (1967) attracted nesting queens in Alberta, Canada by setting out cubical plywood boxes roughly 6 in (15.2 cm) on all sides (Fig. 8.3). The plywood was $\frac{3}{4}$ in (1.9 cm) thick. The entrance holes were $\frac{5}{8}$ in (1.6 cm) in diameter which permitted entry to bees but excluded mice. The boxes had hinged lids and were filled with upholsterers' cotton which the bees used to line their nests. Boxes were fastened to posts with wire to keep skunks from turning them over. Hobbs (1967) favoured a 'false underground' nest, a regular nest box that is set on the ground but modified by using a 1-ft (30.5 cm) section of plastic pipe as an entrance tunnel (Fig. 8.4) and placing a piece of sod over the pipe in such a way as to leave pipe entrance exposed (Fig. 8.5). Presumably the sod gives the illusion that the pipe tunnel leads to an underground nest. Acceptance by queens was highest when the boxes were placed in fallow backyard gardens,

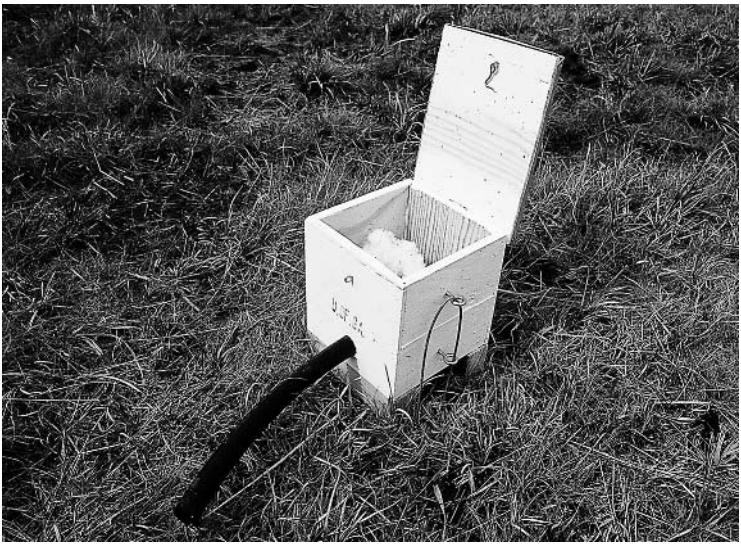


Fig. 8.4. A false-underground bumble bee box after Hobbs (1967). It is similar to an above-ground box except for a section of plastic pipe leading from the entrance. The lid is open to reveal the upholsterers' cotton within. (Source: Keith S. Delaplane.)

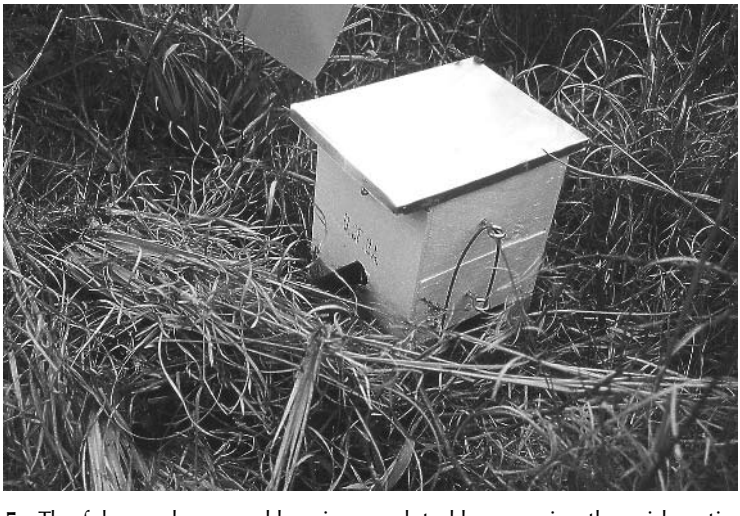


Fig. 8.5. The false-underground box is completed by covering the mid-section of the plastic pipe with soil or sod. This creates the illusion that the exposed end of the plastic pipe is leading to a subterranean cavity. (Source: Keith S. Delaplane.)

beside fence posts in a prairie, and along thickets of small aspen trees. Bumble bee occupancy over 6 years averaged 44±23%. Macfarlane *et al.* (1983) achieved about 30–60% bee occupancy with a slightly different box design in New Zealand. Occupancy of artificial nest boxes in Washington averaged only about 1% (D.F. Mayer, unpublished data), and occupancy in Georgia was zero after a two-season trial (K.S. Delaplane, unpublished data). It seems that artificial nest boxes are most useful in areas where a shortage of natural nest sites is a limiting factor to bumble bee populations.

In order for bumble bee nest boxes to be useful for crop pollination, it is important to set out boxes near the crop of interest or to relocate occupied boxes near to the crop. However, moving nests causes a loss of foragers (presumably because some spend the night in the field) and provokes queens to revert to foraging behaviour which increases the chance of their loss. Colonies that are moved produce fewer queens. Nevertheless, if one can achieve a reasonably good occupancy rate, then this practice may be able to increase bumble bee numbers at a crop. Relocating bumble bee boxes should be limited to crops that bloom relatively late in the season because this allows more time for colonies to recover an adequate foraging force.

One could conceivably increase the population of bumble bees in an area over time by repeatedly introducing bumble bee colonies which release new queens at season's-end. With similar objectives, Clifford (1973) increased peak densities of local bumble bee populations by importing and releasing 100 queens each spring for 3 years; however, bee densities returned to their previous levels when queen importations stopped.

Rearing bumble bees year-round

The keys to rearing bumble bees year-round are: (i) inducing queens and males to mate in captivity; (ii) bypassing or abbreviating the queen's natural diapause interval; (iii) inducing queens to rear a brood in captivity; (iv) growing colonies so that they produce a foraging force of workers; and (v) retaining some queens and males in order to start the cycle over again. A few companies rear bumble bees efficiently on a large commercial scale, but their methods are held as proprietary secrets. Nevertheless, the scientific literature gives some information on bumble bee-keeping from which we made the following summary, supplemented by our own experiences (Plowright and Jay, 1966; Heinrich, 1979; Pomeroy and Plowright, 1980; Röseler, 1985; Griffin *et al.*, 1991; van den Eijnde *et al.*, 1991; Tasei, 1994; Tasei and Aupinel, 1994; and S.A. Cameron, unpublished report). Different bumble bee species have different optimal rearing conditions, and some

simply take to domestication easier than others. Therefore, the following sections provide only a general guideline.

Honey bees as a source of pollen and surrogate workers

It is useful to have on hand one or two colonies of honey bees (see Chapter 6) with pollen traps (see Appendix 1). Honey bee hives thus fitted can provide fresh bee-collected pollen for feeding the bumble bees. Pollen must be collected daily from the trap and immediately frozen. It is important to collect and freeze enough pollen to sustain the operation during winter if it is intended to grow bumble bees year-round.

Young queens of the European bumble bee species *Bombus terrestris* can be stimulated to begin brooding when they are housed with young honey bees; in these cases, honey bee hives are necessary to provide these surrogate workers. Surrogate honey bee workers are apparently not helpful for rearing North American bumble bees.

Fig. 8.6. A two-chamber queen starter box opened to reveal its components. A partition separates the chambers but has a passageway in order to allow bees to move between chambers. The chamber at the left is the feeding/defaecating chamber. There is a hole in the lid to accommodate a vial of syrup or honey water. The floor is lined with disposable corrugated cardboard. A plastic lid on the floor catches drips. The nest chamber at right has upholsterers' cotton and a plastic lid with a ball of pollen dough. A transparent Plexiglass inner cover allows the beekeeper to inspect the nest chamber with minimal disturbance to the bees. (Source: Nancy B. Evelyn.)

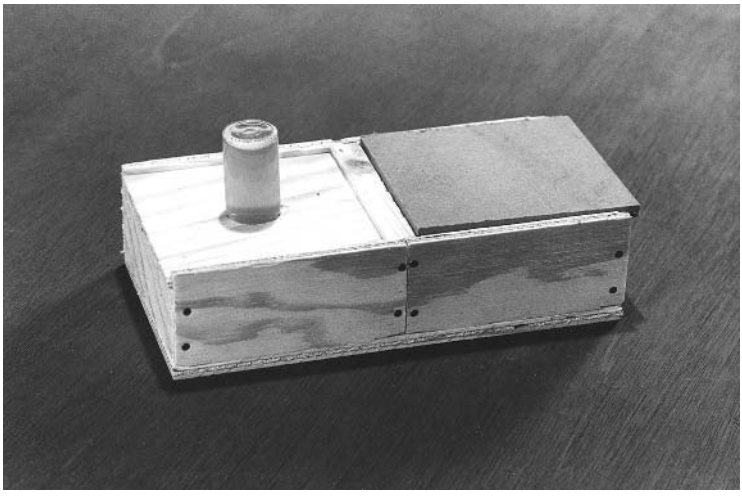


Fig. 8.7. An assembled two-chamber starter box. A piece of hardboard covers the Plexiglass inner cover of the nest chamber. (Source: Nancy B. Evelyn.)

Surrogate honey bee workers should be used only when they are less than 12 h old. To harvest these young workers, one must open a honey bee hive and look for a comb of emerging worker bees. Combs of emerging bees contain a large quantity of capped brood and upon close examination one can see the ragged edges of recently-opened cells. Light-coloured young bees (< 12 h old) will be walking on the comb, and one may see bees emerging from cells. When such a comb is identified, it is brushed free of all adhering bees and placed inside a white plastic bag and stored overnight at comfortably warm temperatures. The next morning there will be numerous young bees walking around in the bag. As long as the bag does not overheat and contains some honey from the comb, the bees can remain there until they are added to the bumble bee queen starter boxes within the next few hours.

The queen starter box

Queen starter boxes are small boxes in which mated queens are placed and induced to begin nesting. Reported dimensions are variable and probably do not matter greatly. One design is a box ~9 × 4.5 × 2 in (22.9 × 11.4 × 5 cm) with two chambers – a nest chamber and a feeding/defaecating chamber (Figs 8.6 and 8.7). This design keeps the box interiors dark, but the nest chamber can be easily opened and bees observed through the clear inner cover (light bothers some bumble bee species; others do not seem to object to it).

The floor of the defaecating chamber can be made of small-mesh hardware cloth or be lined with a square of corrugated cardboard that is replaced as needed. In one design, there is no permanent floor in the defaecating chamber and instead a piece of cardboard or heavy blotting paper is taped to the bottom of the box and replaced as needed. Bees can pass between the nesting and defaecating chambers through a small circular opening. A defaecating area that is separate from the nesting area helps maintain general nest sanitation.

Some authors use single-chamber starter boxes. One such design is a ~4.75 × 2.25 × 4.25 in (12 × 5.5 × 11 cm) box with transparent Plexiglass side walls, and another is a ~4.5 × 1.75 × 1.75 in (11.3 × 4.5 × 4.3 cm) box with a Plexiglass lid.

Regardless of the design chosen, it is helpful to provide each box with a small plastic lid in the nest chamber on which pollen will be provided and the queen will build her brood clump. By encouraging the queen to nest on a plastic lid, it is a relatively simple matter to move the comb later when the incipient colony is graduating up to a finisher box. It is also helpful to attach a plastic honey bee queen grafting cup (see Appendix 1) to the floor of the plastic lid with melted beeswax; these cups simulate the shape and size of a natural bumble bee honey pot and may encourage nesting (Fig. 8.8).

A small wad of upholsterers' cotton should be placed in the nest chamber; the queen will fashion the material into a fibrous shell

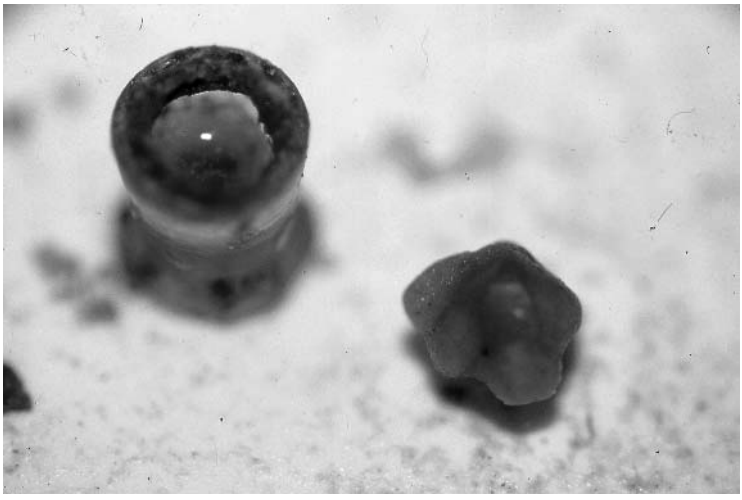


Fig. 8.8. A plastic honey bee queen grafting cup (top left) simulates the size of a natural bumble bee honey pot and may encourage nesting. The brood clump (bottom right) has five brood cells that look like bulges off the central core of pollen. Under each bulge are developing eggs or larvae. (Source: Keith S. Delaplane.)

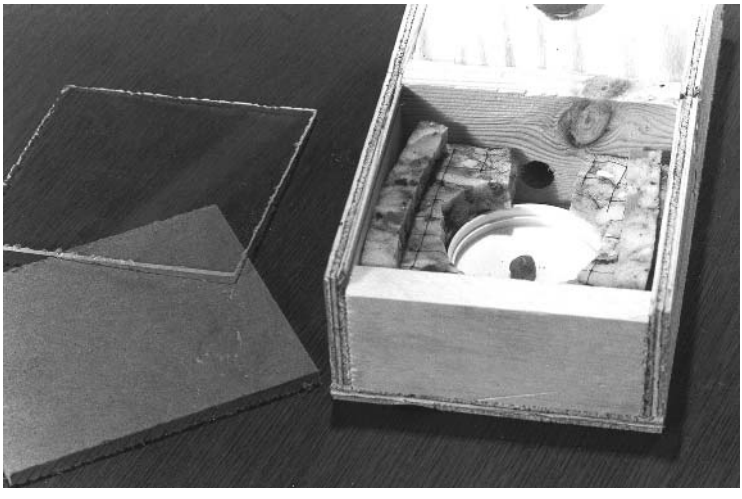


Fig. 8.9. A nest chamber with chip foam (carpet padding) instead of upholsterers' cotton. By cutting out holes in layers of chip foam, one can make a cavity for the pollen ball that is enclosed yet easily accessible. (Source: Nancy B. Evelyn.)

around her comb. Some authors recommend chip foam (carpet padding) instead of upholsterers' cotton. It is easier to handle and replace than upholsterers' cotton. By cutting out holes in layers of chip foam, one can make a cavity for the pollen ball that is enclosed yet easily accessible (Fig. 8.9).

Some kind of gravity feeder for dispensing syrup or diluted honey should be inserted through the lid or wall of the feeding/defaecating chamber. The feeder can be a pipette with one end sealed off or a small inverted vial with a tiny perforation in its lid from which bees can drink. Another feeder design is a block of solid plastic with numerous feeding wells drilled into it. The wells are filled with syrup and the block placed in the feeding/defaecating chamber. Feeders should be cleaned at least after every third filling.

The finisher box

Queens that successfully rear brood in starter boxes must soon be transferred to larger finisher boxes in which the colony can grow to maturity. Conceivably, one could bypass the starter boxes but their failure rate is moderate to high and it makes sense to use small containers that take up less space for that early precarious stage. Like starter boxes, published designs for finisher boxes are variable. Outside dimensions for one design are ~11.75 × 8.25 × 6.75 in

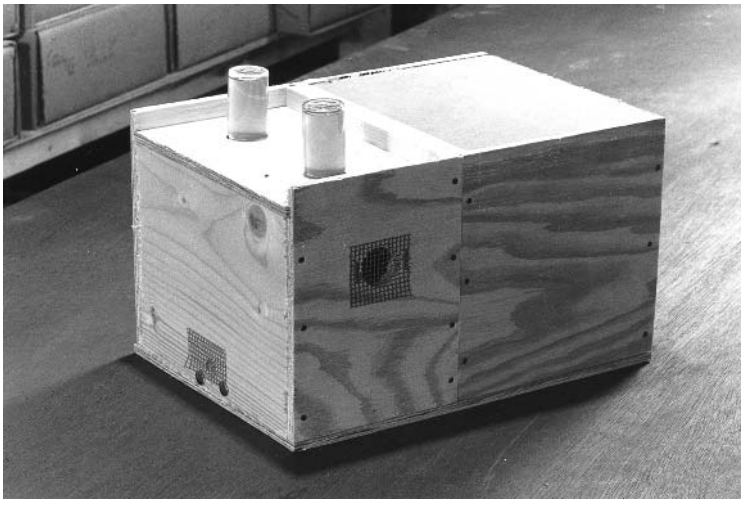


Fig. 8.10. A two-chamber finisher box designed to accommodate a queen and her growing colony. There are ventilation holes covered with hardware cloth in the side walls of the feeding/defaecating chamber and a flight entrance, closed in this photograph with hardware cloth and thumb tacks. (Source: Nancy B. Evelyn.)

(30 × 21 × 17.5 cm). There are separate chambers, but this time the nesting chamber is larger than the feeding/defaecating chamber. Ventilation is provided by holes drilled in the walls of the feeding/defaecating chamber and covered with hardware cloth (Fig. 8.10). Floors of the defaecating chamber can be made of metal mesh or lined with some kind of disposable absorbent material. The feeding/defaecating chamber must have a gravity syrup feeder.

It is ideal if the floor of the nest chamber is sloped upward, like an inverted cone, at angles of 35°. This design conforms to the natural shape of a growing bumble bee comb. One author achieves this effect by moulding nests of the correct shape out of porous concrete. Another way to do this is to lay several layers of carpet padding inside the nest chamber. A hole is cut out of the centre of each layer of carpet padding, each hole successively larger than the one below (Fig. 8.11).

Ambient rearing conditions

It is important to provide favourable climate conditions for starter boxes and finisher boxes. Some authors maintain rearing rooms at ~82.4–86°F (28–30°C), 50–65% relative humidity, and in total darkness. Some light-sensitive species do better if the area is illuminated

with red light while the operator is feeding or inspecting the young colonies. Species that are not light sensitive do not need dark rearing rooms, but even with these species it is advisable to use boxes that are designed to keep interiors dark.

One option to humidifying the room is to humidify each starter box. One can do this by placing damp filter paper just under the lid of the nest chamber. This works best in finisher boxes provisioned with chip foam instead of upholsterers' cotton (Fig. 8.12). The damp paper must be changed daily to avoid mould problems.

Feeding colonies in captivity

Fresh food must be prepared at the same time the incipient colonies are being started. A syrup made of 1 part sugar to 1 part water is prepared and placed in the gravity feeders. Some authors recommend putting the antibiotic Fumidil® B (see Appendix 1) in the syrup to control nosema disease. One option to sugar is a syrup made of 1 part honey to 1 part water. Honey syrup ferments more rapidly than sugar syrup and must be replaced more frequently (at least every 2 days), but bees can locate it more easily because of its attractive odour.

Fresh bee-collected pollen must be cleaned of visible debris, ground into a fine consistency, and added to sugar or honey syrup

Fig. 8.11. A finisher box opened to reveal the floor of the nest chamber. A hole is cut out of the centre of each layer of carpet padding, each hole successively larger than the one below, in order to create a cavity suitably-shaped for a growing brood comb. (Source: Nancy B. Evelyn.)

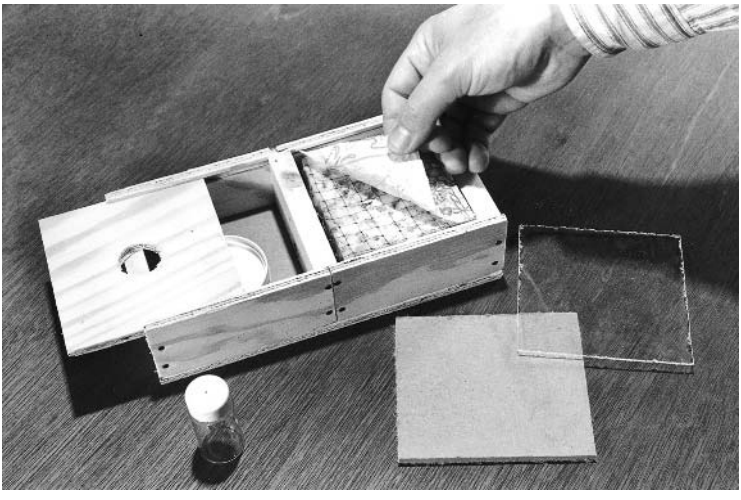


Fig. 8.12. A damp filter paper just under the lid of the nest chamber is one way to humidify a starter box. It must be changed daily to avoid mould. (Source: Nancy B. Evelyn.)

until it achieves a dry dough-like consistency. Pollen must be kept fresh-frozen in its bee-collected pellet form until it is needed. Queens produced from colonies that are fed fresh-frozen pollen are larger, have lower mortality rate, and produce larger colonies than do queens produced from colonies fed dried-frozen pollen (Ribeiro *et al.*, 1996).

Catching queens and initiating nests

Queen bumble bees become active and fly on warm days in spring when early pollen sources become available. It is best to catch them while they are still searching for a nest site and have not yet started a nest; one can find such queens flying low to the ground in a zig-zag pattern obviously exhibiting searching behaviour. Queens with pollen on their legs have already started a nest in the field and are unlikely to resume nesting in captivity.

Queens can be caught with an insect net. They should be transported individually in small jars padded inside with paper towelling and with lids loosened to provide ventilation and prevent overheating. They should be transferred to starter boxes as quickly as possible.

Bumble bee queens are placed individually in starter boxes. In the case of *B. terrestris*, each queen can be given three or four young honey bees as surrogate workers. A bean-sized lump of pollen dough

is placed on the plastic lid in the nest chamber and close to the artificial honey pot. Gravity feeders and the artificial honey pot are filled with syrup. Starter boxes are placed in proper temperature and humidity conditions and left undisturbed for at least 24 h after which the queens are checked for nesting activity. Promising signs are (more-or-less in this order): wax deposits on the floor; wax deposits on the plastic honey pot; a natural wax honey pot; natural honey pots filled with syrup; excavations on the pollen lump; and a *brood cell* in the pollen lump (Fig. 8.8). A brood cell looks like a bulge on the side of the pollen lump. The queen excavates a depression in the pollen lump, lays one or more eggs in it, and covers the eggs with a dome of wax. Under this dome each egg may be partitioned from its neighbour or all eggs may be grouped together, depending on the species. The pollen lump can now be referred to as a *brood clump*.

If after 24 h there are no signs of nesting activity, the pollen lump should be replaced and the queen left alone for another 24 h. Faeces in the defaecation chamber indicates that the queen is eating pollen and may eventually lay eggs. Once the queen starts making brood cells, new pollen dough lumps should be placed next to the brood clump three times a week. However, overfeeding is a common problem and a queen should not be fed more than she consumes. A good guideline is to feed no more pollen dough than one-third the volume of the brood clump. If the brood clump does not grow, this indicates that the larvae may be dead or that the young colony is being underfed. Any uneaten food must be removed regularly.

Graduating incipient colonies to finisher boxes

After the first worker bumble bees emerge, the queen, workers, and brood clump can be transferred into a finisher box. The brood clump, plastic lid base and all, is placed in the centre of the nest chamber floor of the finisher box. The growing colony continues receiving syrup and pollen lumps, and the quantity is gradually increased as the colony grows. At this stage, some species will readily accept natural pollen pellets as collected from the pollen trap; this saves the labour of making pollen dough. The pollen pellets can be simply sprinkled on top of the brood clump. It remains important to avoid overfeeding and to cut back on food if uneaten pollen accumulates in the nest.

Graduating colonies into pollination units

A finisher box colony is ready to go outside for free flight and pollination as soon as it has around 80 worker bumble bees. It is helpful to

continue feeding colonies pollen and syrup for a few days to help colonies through this transition period. Four colonies can be housed together in one box, each colony partitioned from the others and with a separate flight exit. Colonies can be placed in the field or orchard in a manner similar to that for honey bees (see Chapter 7, page 55). Colonies should rest on concrete blocks to keep them off the ground, and they should be secured to tree trunks or posts so that they cannot be overturned by skunks or other predators.

Mating queens and inducing hibernation

For year-round production of bumble bee colonies, it is necessary to prepare a flight room or mating cage in which males and queens can mate. The flight room should be ~12 × 19 ft (3.7 × 5.8 m) in size and warm and sunny. A sunny porch or similar screened enclosure can suffice. Some bumble bee species will mate in small cages covered with gauze or wire mesh. In these cases, the mating cage should be ~20 × 20 × 20 in (70 × 70 × 70 cm). Whether using a cage or a flight room, the enclosure must be provisioned with shallow pans of syrup and pollen, and a shallow pile of moistened peat moss or soil must be deposited on the floor and covered with a layer of raw cotton, straw, or dry leaves. If a flight room is used, bees seem to find the food more easily if it is placed on a window sill.

Fig. 8.13. Queens are placed individually in vials half-full of damp peat moss and refrigerated for up to 8 months. (Source: Keith S. Delaplane.)

To maintain year-round production, one must induce new queens and males from cultured colonies to mate in captivity. In appearance, males have longer antennae, more barrel-shaped abdomens, and more variable body coloration compared with workers (Fig. 8.1). New queens are noticeably larger than workers and more brightly coloured (Fig. 8.2). Queens and males are produced after the colony has reached maturity. To induce mating, queens and males from two or more colonies are released in the flight room. Ideally, there should be about twice as many males as females, and the bees should be released in the morning. After the queens mate they invariably will bury themselves in the soil on the flight room floor. The bee-keeper can then dig out these queens, place each one individually in a vial half-full of damp peat moss (Fig. 8.13), and store them at normal refrigeration temperatures (~41°F, 5°C). The vials and peat moss should be heat-sterilized to reduce mould problems.

Activating second-generation queens

The length of the hibernation period, or lack thereof, represents the flexible stage in bumble bee culture that permits year-round availability of colonies. The queen's hibernation period can be eliminated or truncated according to the demand for colonies. A necessary tool for this step is a canister of carbon dioxide (CO_2) gas with a regulator connected to a few feet of rubber tubing. CO_2 acts as an anaesthesia and egg-laying stimulant in bees.

If one wishes to resume rearing colonies immediately, the hibernation period must be circumvented. Queens are not refrigerated after they dig into the soil in the flight room, but instead one day after mating are placed individually in a glass jar in which each is treated with CO_2 until she is immobilized. The queen is kept in the closed jar for 30 min then returned to the flight room or mating cage and provided syrup and pollen pellets. The CO_2 treatment is repeated after 24 h. Two to four days after the last CO_2 treatment, each queen is placed in a starter box as before.

If a period of hibernation is desired, then queens can be kept refrigerated in their peat-filled vials for up to eight months. To activate refrigerated queens, CO_2 is injected directly into each vial for 10 s, then the queens are moved to a slightly elevated temperature (59°F, 15°C) for overnight. In the morning the queen vials, still closed, are moved into the flight room or mating cage at room temperature. Two or three hours later, queens are released so that they can fly and the room is provisioned with syrup and pollen pellets. After several minutes of flight, each queen is placed individually in a jar and treated with CO_2 for 30 min. Queens are returned to the flight room and the

CO_2 treatment is repeated the next day. Three to 6 days after the last CO_2 treatment, each queen is placed in a starter box as before.

It is very important that activating queens fly and eat pollen and syrup. If they are sluggish in the flight cages and do not visit feeders, it may help to house them individually in queen starter boxes provisioned with pollen pellets and syrup; this may help focus their attention on food. Some growers believe that single-chamber starter boxes help focus bees' attention on food even more. At least once a day each queen should be encouraged to fly in the flight cage until she shows brooding behaviour in the starter box, at which point she should remain confined to the starter box.

Managing Hived Bumble Bees for Pollination

Many of the principles of hive placement discussed for honey bees (see Chapter 7, page 55) apply also to hived bumble bees used for field pollination. Although bumble bees frequently forage long distances from their nests (Dramstad, 1996; Saville *et al.*, 1997; Osborne *et al.*, 1999), bumble bees from commercial hives placed in apple and pear orchards foraged optimally at relatively short distances, within 60 ft (18.3 m) of the hive (Mayer and Lunden, 1997). If the Mayer and Lunden data are representative of foraging patterns under commercial pollination conditions, this means that pollination will be optimized when hives are numerous and well dispersed in an orchard. Meeting this goal in field conditions may be difficult because commercial bumble bee hives are expensive.

Bumble bees are easily stressed after moving. Workers may get lost when they leave the nest for the first time, and queens may abandon the nest. To reduce these problems, one can mark hive entrances with distinguishing designs so that workers can visually orientate to their home hive. To discourage queens from leaving, it is important not to move colonies until there are at least 80 workers or, at the very earliest, the second batch of brood has emerged. It may help to feed colonies syrup and pollen for a day or two. Outdoor colonies can gain some protection from parasitic cuckoo bees (*Psithyrus* spp.) if the beekeeper uses small entrances. Sladen (1912) used a small entrance of the dimensions $\frac{9}{32} \times \frac{7}{16} \times \frac{3}{8}$ in ($0.7 \times 1.1 \times 1.0$ cm) to exclude mice, and he 'reduced the size of the hole in the mouse-excluder' to exclude cuckoo bees. Colonies can be protected from skunks and other predators by mounting them on elevated stands or wiring them to posts or trees.

Bumble bees have distinguished themselves as pollinators of glasshouse plants, especially tomato (Banda and Paxton, 1991; van Ravestijn and van der Sande, 1991; Pressman *et al.*, 1999). Colonies in

glasshouses should be fed syrup continuously. Little published information exists on recommended hive densities in glasshouses, but rates as high as six colonies per acre (15 ha^{-1}) have been used (van Ravestijn and van der Sande, 1991).

Chapter 9

Alkali Bees

Biology

The alkali bee (*Nomia melanderi*, family Halictidae) is a valuable pollinator in lucerne and onion seed production. It is a solitary soil-nester and occurs naturally in limited areas west of the Rocky Mountains in North America. It nests gregariously, often in huge concentrations (Mayer and Miliczky, 1998). Each female makes and provisions her own nest with no contact between larvae and other adults. In nature, nesting is confined to places where the soil is sub-irrigated over a hardpan layer which leads to relatively bare alkali spots.

The original description of the species was based on a specimen collected at Yakima, Washington. Adults are about two-thirds the size of a worker honey bee and are black with metallic-coloured bluish, greenish, or yellowish bands circling the abdomen. Females (Fig. 9.1) have stingers but rarely use them. Males have white-coloured faces and long pointed antennae (Fig. 9.2).

Alkali bee adults emerge from the soil in late spring or early summer, depending on temperature and moisture of the soil. Emergence is delayed if temperatures are cool or the ground is very wet. Adults generally emerge during the late morning. The active season varies from late May to mid-August in Washington, from early June to early September in Idaho, and from late May to early September in Oregon. Adults have been collected as early as 15 April (Utah) and as late as 6 November (Washington). Females begin nesting soon after they mate. They prefer to use pre-existing holes in the ground.

The nest consists of a vertical shaft with a lateral tunnel that has oval cells branching from it (Fig. 9.3). Cells may be as deep as 12 in (30.5 cm) below the surface, but most are 2–8 in (5.1–20.3 cm). They are deeper during dry seasons and shallower during wet seasons. Females line cells with a moisture-resistant glandular secretion. Soil

Fig. 9.1. A female alkali bee, *Nomia melanderi*. (Source: Daniel F. Mayer.)

removed from the nest is deposited around the entrance hole to form a mound with a hard central turret.

Females eat nectar, and about 2–3 days after emergence begin collecting pollen to provision a nest. Pollen is placed at the bottom of each cell in a round flattened ball about $\frac{1}{4}$ in (0.6 cm) in diameter and

Fig. 9.2. A male alkali bee, *Nomia melanderi*. (Source: Daniel F. Mayer.)

Fig. 9.3. General design of subterranean nests of alkali bees and other soil nesters. (Source: Darrell Rainey.)

$\frac{1}{8}$ in (0.3 cm) thick. Females 1–4 weeks old collect enough pollen each day to provision one cell. At night the egg is laid, the cell is plugged, and a new cell prepared for the next day's pollen collection. Eggs are found in cells in Washington from about 17 June to 26 July. Eggs hatch in 2–3 days and larvae consume all the pollen ball in 7–10 days, growing progressively larger.

There are five instars, and feeding larvae are found in cells in Washington from about 23 June to 14 August. The fifth instar is divided into the predefaecating stage and the prepupal stage. During the

Fig. 9.4. Prepupa of the alkali bee. (Source: Darrell Rainey.)

predefaecating stage of 4–6 days, the body appears bloated and brown faeces are visible inside the larva. Larvae defaecate by smearing faeces on the sides of the cell wall over 2–3 days. The prepupa is opaque white, has a sharp angle between the head and the thorax, and has prominent humps on the back (Fig. 9.4). This is the overwintering diapause stage of the alkali bee which lasts 10–11 months. Prepupae are first found in cells from about 3–9 July.

Increasing soil temperature in spring breaks diapause and the prepupa changes to the pupa around the end of May. This stage lasts 15–20 days, with the pupa gradually becoming coloured more like an adult. The pupa changes to the adult which remains in the cell for a short time before digging to the surface. This generally occurs during June. Individual females live 4–6 weeks. Females will be present and active in a given area for about 60 days under good weather conditions.

Alkali Bees as Pollinators

The native alkali bee is a major pollinator of the introduced lucerne plant and enjoyed its heyday in the 1960s and 1970s before alfalfa leafcutting bees became widely used as pollinators (Bohart, 1972; Torchio, 1987).

An alkali bee female trips at least 95% of the lucerne flowers she visits as she gathers pollen for her nest. Under good conditions, each female will trip about 25,000 lucerne flowers during her lifetime which translates to $\frac{1}{5}$–$\frac{1}{2}$ lb (91–227 g) of clean seed. Females tend to forage within 1 mile (1.6 km) of the nest, although they have been found up to 7 miles (11 km) from the nest.

Compared to other lucerne pollinators, alkali bees work more blooms in the dense lower foliage, seek more untripped flowers (Batra, 1976), and fly in cooler, windier weather. Compared to honey bees, alkali bees visit and pollinate more lucerne flowers on a per-bee basis. Alkali bees prefer lucerne for its pollen whereas honey bees prefer it for its nectar (Torchio, 1966). Alkali bees work lucerne equally well in fields that are water stressed or well watered, but honey bees have trouble tripping flowers in well-watered fields. Thus, pollination with honey bees requires more careful water management to provide optimum pollination conditions. This is an important advantage to alkali bees in areas like the San Joaquin Valley of California where water stress is difficult to manage (Wichelns *et al.*, 1992).

The value of alkali bees was highlighted in a case history from a central California water district (Wichelns *et al.*, 1992). During the 1960s, several lucerne growers began installing artificial alkali bee beds and importing bees from Washington and Oregon. During this

time, average seed yields jumped from 560 lb acre^{-1} (627 kg ha^{-1}) in 1960 to 950 lb acre^{-1} (1064 kg ha^{-1}) in 1971. But in 1970/71 alkali bee populations declined sharply; possible causes were insecticide applications in the area, insecticide residues in the water used to dampen bee beds, and bee parasites. Lucerne yield and acreage declined rapidly thereafter, and lucerne acreage has not yet recovered to pre-1971 levels. Thus, we see the rise and fall of a local lucerne industry coincidental with the presence of alkali bees.

Today alkali bees are largely supplanted as commercial pollinators by the exotic alfalfa leafcutting bee. However, for two or more decades theirs was a remarkable case history of 'a new pollinator brought up from the ranks of native bees' and 'domesticated' for commercial pollination purposes (Buchmann and Nabhan, 1996). Moreover, alkali bees are the only soil-nesting bee native to North America for which practical, large-scale management practices have been developed. Thus, alkali bees are a valuable natural resource for agriculture in the western US. In the interest of preserving this natural resource we include in this chapter detailed instructions for their management.

Recommended Bee Densities

The number of foraging female bees required in a lucerne field is not fully known, but it should probably exceed 3000 acre^{-1} (7410 ha^{-1}). It is easier to measure bee densities by assessing nest concentration. A good natural nesting site will average about 1 million nests acre^{-1} (2.5 million ha^{-1}). One acre (0.4 ha) of bed with this number of nests should provide for 1000 lb of clean seed acre^{-1} (1120 kg ha^{-1}) on 200 acres (81 ha) of lucerne. The maximum population in artificial beds is about 5½ million nests acre^{-1} (13.6 million ha^{-1}). Estimates of nest concentration can be made on the basis that 23, 46, and 69 nest holes ft^{-2} represent 1, 2, and 3 million nests acre^{-1}, respectively (2.5, 4.9, and 7.4 holes dm^{-2} represent 2.5, 4.9, and 7.4 million nests ha^{-1}, respectively).

There is a simple sampling method that works reasonably well for estimating the value of a bee bed. While walking along a line across the bed, an observer takes ten or more random counts of the number of nests per square foot or square decimetre. The more counts, the better the estimate. After finding the average number per square foot, it is multiplied by ten to derive the average number of nests 10 ft^{-2}. To find average number of nests per square metre, the number per square decimetre is multiplied by 100. This figure is inserted into the formula below to determine a Pollination Index (PI).

$$PI = no.\ nests\ 10\ ft^{-2} \times acres\ of\ bed \times \frac{200}{acres\ served}$$

or

$$PI = no.\ nests\ m^{-2} \times ha\ of\ bed \times \frac{186}{ha\ served}$$

An index value of 230 indicates an adequate number of pollinators; values above 230 are good to excellent, and values below this are fair to poor.

If one is planning a semi-artificial or artificial bee bed (see pages 92–93), there is a different form of this formula useful for estimating the required size of a bed for a given area of lucerne. Using a recommended PI value (say, at least 230), a recommended target density of nest holes per ten square feet (say 230) or square metre (say 250), and the known area of lucerne to be served – these values can be inserted in the following formula to determine the required size of bee bed.

$$Required\ size\ of\ bee\ bed\ (acres) = \frac{PI \times acres\ served}{200 \times target\ nest\ 10\ ft^{-2}}$$

or

$$Required\ size\ of\ bee\ bed\ (ha) = \frac{PI \times ha\ served}{186 \times target\ nest\ m^{-2}}$$

It takes time for new nesting sites to fill up with a full complement of larvae. A new bed in southeastern Washington had a mass fly-in of nesting females in 1976 which provided up to 70 nest entrances per square foot (7.5 dm^{-2}) the first season. However, there were only one-fourth as many progeny as in older sites. New sites usually require at least three favourable seasons to develop good production. Artificial beds often produce two to three times as many progeny per unit soil volume as do managed natural sites. However, they are more variable and do not maintain peak populations without periodic renovation or expansion.

Three hundred healthy prepupae per cubic foot (106 dm^{-3}) is excellent production and 200 (71 dm^{-3}) is good. Since more males than females are produced, the local increase in females is comparatively slower than that for males. It takes time for alkali bees to repopulate an area following a natural or man-made disaster. In 1973, several beds in southeastern Washington were reduced to about ten prepupae per cubic foot (3.5 dm^{-3}) after an insecticide poisoning. By

the end of the 1974 season, they had increased a little over four-fold. With poor weather for reproduction in 1979 they remained about the same – 17–45% of a good population.

Qualities of Good Nesting Sites

There are three important factors determining the quality of alkali bee nesting sites, whether natural or managed: (i) soil moisture; (ii) soil composition and texture; and (iii) vegetation. The first two are discussed in this section. Vegetation is covered in more detail on page 95.

Soil moisture

Soil must be moist down to at least 12 in (31 cm). Soil moisture in good sites varies from 8 to 32% depending on soil type. Soil moisture can be measured using a tensiometer. A reading of 15–25 centibars indicates adequate moisture regardless of soil texture.

Dry nesting sites have been a limiting factor in alkali bee production. Good natural moisture conditions are associated with shallow layers of calcareous hardpans lying a few inches to several feet below the surface. Seepage water may sub-irrigate nearby nesting sites when a shelf of this impervious material lies along a river, canal, or pond. Where this occurs, populations of alkali bees may build up naturally with little management. Most nesting sites are man-made and require an artificial water supply provided with shallow ditches dug across or around beds, or some kind of subsurface distribution system (see page 91).

Soil composition and texture

Maintaining proper soil texture in alkali bee beds is almost as important as providing adequate water. These two factors are interrelated. A soil of poor texture can limit the movement of water through the upper horizon even when water is abundant. Conversely, soil of excellent textural qualities is of little value where water is in short supply.

Proper soil texture encourages excavation by bees and allows continuous capillary flow of subsurface water towards the surface, replacing water in the upper layers at a rate equal to or slightly greater than the rate of evaporation. The surface should not be crusty or fluffy. The goal of soil texture management is a moist and moderately compact upper soil horizon which persists throughout the active bee season.

Uniform soil moisture and good nest digging conditions depend largely on the percentage composition of clay, sand, and silt, with clay preventing capillarity at levels greater than 25%. Soils high in sand (45–80%) are difficult to seal, and excessive water movement and evaporation may occur. The likely result is a wet bed with a dry, powdery surface. Sandy beds become quickly populated with maximum numbers of nesting bees but do not maintain good populations for more than 3–4 years. The best alkali bee beds have soil classed as silt loams with 2–6% fine silt and 42–68% coarse silt. They contain 13–24% clay and 10–40% sand.

Vegetation

The surface should be essentially bare with sparse vegetation. Plants use up soil moisture and bees prefer to nest in bare ground. Nevertheless, a little vegetation can help protect bees from summer rains and reduce wind erosion. See page 95.

Building or Enhancing Bee Beds

Until the late 1950s, most nesting sites were of two basic types – *natural* and *semi-natural* or totally *artificial*. Beginning around 1958, growers in Washington developed a third type – the *semi-artificial* bed.

Natural and semi-natural (open-ditched) beds

Many areas in the Great Basin of the northwestern US are naturally ideal for alkali bee nesting. Such areas usually occur in low lying regions of larger valleys where subsurface drainage is poor (on alkali spots). Some of these areas support small populations of non-managed alkali bees. Lucerne-growing lands that border on rivers or include large alkali spots may be at a special advantage in regard to pollination.

Auxiliary water supplies may be needed at natural nest sites if there typically is a marked drop in soil moisture during the bee nesting period (a situation common in mid-June to early August in southeastern Washington). One can maintain proper moisture conditions in sloping sites by digging basins 18–36 in (46–91 cm) deep along the upper border of the bed. Water from these reservoirs seeps downhill under the site. Hardpan or caliche layers at 12–18 in (31–46 cm) depth can help direct the lateral movement of water below the surface. It is important not to penetrate these layers when excavating seepage basins.

For beds on level ground, one can dig a series of 12–18 in (31–46 cm) ditches around the perimeter of the bed and at 15-ft (4.6 m) intervals through the middle. The objective is to maintain water in these ditches or basins starting about a month before bee emergence and continuing through most of the nesting period. This is especially important during dry seasons. Flood irrigation water is available throughout the summer at many locations in southwestern Idaho and eastern Oregon. Diverting this water into seepage ditches for bee beds can be fairly easy. In Walla Walla County, Washington, such water supplies are limited or unavailable after mid-June, and auxiliary water must come from wells. Several large and highly productive natural sites in the Touchet-Lowden-Umapine region have near-perfect moisture conditions. Surface moisture at these sites remains at optimum levels throughout the nesting period, and only token auxiliary water supplies are necessary. Ideal situations like this are rare.

Semi-artificial (pipeline) beds

Semi-artificial beds have some important advantages:

- They can be built anywhere there is suitable soil and adequate water supplies.
- Compared to natural beds, they give a grower greater control over a pollination programme.
- They are less expensive to install than artificial beds.

The first step in developing a semi-artificial bed is to determine the size of bed required for the crop acreage to be pollinated (see page 88). The bed must be located as near as possible to the lucerne.

A large and continuous supply of water is necessary for semi-artificial sites. One must plan for 200,000 to 800,000 gal acre^{-1} (1.9–7.5 million l ha^{-1}) to moisten the upper layers of a bed before nesting season. Most growers start adding water in April or May, depending on beginning moisture levels. After nesting begins, smaller amounts of water must be kept flowing in the lines throughout all but the last week of the nesting period.

Trenching can begin when the ground is dry enough to accommodate lightweight equipment. Most growers in the Touchet-Lowden-Umapine area dig trenches 24–30 in (61–76 cm) deep and 6–8 in (15–20 cm) wide. Parallel trenches should be dug across the bed at 8–10 ft (2.4–3.1 m) intervals. This degree of spacing permits water to distribute relatively uniformly.

A number of piping materials can be used. Rigid PVC pipe, $2\frac{1}{2}$–3 in (6.4–7.6 cm) in diameter, is easy to work with and can be easily cut

and joined to other sections with cementing compound. Black flexible plastic piping, 1–1½ in (2.5–3.8 cm) in diameter, is less expensive and can be purchased in large rolls and easily transported to a site. With either piping material, it is necessary to drill one or two ⅜–½ in (1–1.3 cm) holes in the pipes at 6–24 in (15–61 cm) intervals along their full lengths before laying them in the trenches. This allows for an even flow of water into the surrounding bed. Some growers use 3–4 in (7.6–10.2 cm) diameter corrugated polyethylene drainage tubing which comes with 24 perforation slots per foot. For a few cents more per foot, it is possible to get this material with a fine mesh wrap which reduces silting.

A 10 in (25 cm) layer of clean round gravel is laid inside the trench to facilitate movement of water. A thin layer of straw or coarse sand placed over the gravel can help prevent downward movement of fine soil. Rigid PVC piping can be laid flat in the trench on top of the gravel layer. Elbow sections with short vertical pieces that extend to the bed surface are attached at both ends. One vertical end-piece is the downspout; the other is a breather tube. If one is using flexible pipe material, it is laid in the trench so that both ends angle gradually to the bed surface. Pipes should not exceed 100 ft (30.5 m) in length because longer lengths impair good water distribution. Once pipes are in place, soil can be returned to the trenches and watered down to settle the matrix into the trenches. It is important not to use too much water or else fine soil may wash into the gravel area.

A water main must be brought to the new bed from a well or other source. Some system is needed to deliver water equally to all downspouts. Most growers use a mainline supply trunk lying along one edge of the bed with a separate spigot and hose serving each downspout. Watering must begin in May or earlier depending on the dryness of the soil. Large quantities of water will be needed where soil is dry (above 25 centibars).

Artificial (plastic-lined) beds

Artificial bee beds are an effective way to concentrate populations of alkali bees at desired locations. However, there are some important limitations:

- Construction costs per unit area are higher than for semi-artificial beds.
- Because of high costs, artificial beds are usually smaller and generate smaller numbers of bees.
- Moisture management is more difficult in artificial beds. They can quickly become too wet or too dry.

- Artificial beds require renovation more often and tend to go through 'boom and bust' cycles.

First, an artificial nest site must be prepared by excavating soil to a depth of 18–36 in (46–91 cm) with a backhoe. Artificial beds are commonly sized 30 × 60 ft (9 × 18 m) which happens to correspond to the size limit of the commercially-available polyethylene plastic material used to line the floor of beds. Some growers overlap sheets of plastic to increase the size of beds.

The floor of the pit must be carefully levelled once excavation is complete. This helps ensure uniform distribution of water. The floor and sides of the pit are lined with a sheet of 6–8 mil (0.15–0.2 mm) polyethylene plastic. It is very important not to tear the plastic liner from this point on. It must provide an impervious underground reservoir. Clean round gravel, ¾–1 in (2–2.5 cm) in diameter, is spread over the plastic to a depth of 8–12 in (20–30 cm). On top of that goes 2–3 in (5–8 cm) of coarse sand to help protect the gravel from clogging with fine soil.

Concrete or clay downspouts, each 8–10 in (20–25 cm) in diameter, are placed vertically in the bed for adding water. These should extend from the gravel layer on the floor to the surface. Downspouts are set upright on mounds of gravel raised 3–4 in (7.6–10.2 cm) above the rest of the gravel layer. One downspout for every 400–600 ft^2 (37–56 m^2) of bed surface is the recommended density.

Soil of proper texture is then placed into the prepared pit (see page 90). The amount of water that must be added through the standing downspouts depends on the condition of the site in late spring. When a bed is new and the backfill soil is relatively dry, one can estimate the required amount of water on the basis of soil volume in the bed. A bed with optimum amounts of sand and clay should have 20% moisture at the brood cell level (2–8 in, 5.1–20.3 cm) in late spring. It is important to test the moisture level of backfill soil and, if necessary, make cautious amendments. Adding too much water and saturating the nesting ground can cause serious problems, especially if warm weather does not dry the area sufficiently. High moisture levels can delay emergence of bees, encourage growth of pathogenic fungi, and cause female bees to fly away to better locations. In established beds, one watering through the standing downspouts in late May will usually last all season.

Surface moisture

Any of the three types of nesting sites – natural or semi-natural, semi-artificial, and artificial – can be sprinkled with ½–1 in (1.3–2.5 cm) of

water before bees emerge to provide an attractive, dark surface at the start of nesting season. This is advisable only if the surface is excessively dry and if sprinkler action will not harm the soil structure.

Late season moisture

Additional moisture is not needed after bees have finished nesting. If there is subsequent high precipitation during winter and early spring the excessive moisture levels can increase the rate of prepupal deaths. It is preferable to let sites dry out during late summer to reduce microbial growth and spoilage problems.

Surface salting

Evaporation causes alkali spots to develop on the soil surface of natural beds due to the deposition of salts. The salt is beneficial because it seals in moisture and reduces weed growth. Supplemental sodium chloride (common salt) surface applications are required at about 1 lb ft^{-2} (4.8 kg m^{-2}) in the soils of southeastern Washington. New sites may require up to twice that rate. An annual $\frac{1}{8}$–$\frac{1}{2}$ lb ft^{-2} (0.6–2.4 kg m^{-2}) application is usually sufficient for maintaining established beds. A light, fluffy soil layer on the surface indicates high calcium content and a need for sodium salts. Soils naturally high in sodium become too hard and crusty if salt is added to them.

Vegetation management

Alkali bee nest sites should be essentially bare with, at most, only a sparse cover of vegetation. Heavy plant growth can interfere with nesting activity and use up soil moisture. Roots can penetrate cells, killing prepupae. However, a little plant growth, preferably in strips, is desirable because it helps protect bees from wind and rain. Chemical herbicides are the most effective way to control weeds. Heavy applications of long lasting residual soil herbicides do not seem to harm any stage of the alkali bee.

Although lucerne is one of their preferred plants, alkali bees will visit many plants such as bull thistle, Canada thistle, clover, dodder, dog fennel, goldenrod, mint, morning glory, rabbitbrush, Russian knapweed, saltcedar, sweet clover, and wild carrot. Large concentrations of these competing flowers can dilute the numbers of alkali bees in lucerne. One example of this problem is perennial pepperweed

(*Lepidium latifolium*) which grows in large concentrations in parts of the Yakima Valley, Washington. Mowing and herbicides are one way to deal with competing bloom. However, removing competing bloom is controversial, especially if there are other crops and their pollinating bees in the area that could benefit from the bee pasture (see Chapter 4, page 30 and Chapter 7, page 57).

Attracting and establishing bees

The final and critical step in developing a new bed is establishing a population of bees. This may be easy if the new site is close to existing beds which support large and growing bee populations. Surplus bees from these established sites will move to the freshly prepared surfaces which are relatively clear of vegetation.

If a new bed is isolated from existing populations, bees must be introduced to the area either as adults or as immatures. Several methods have been developed for transplanting bees from one location to another, sometimes over great distances.

Investigators in Utah successfully transferred adult females to new beds (Parker and Potter, 1974). They captured bees at existing sites, anaesthetized them with carbon dioxide, and transported them in an ice chest to new locations. Starter holes were punched in the bed surface to encourage nesting. Bee nesting was optimized when females were released after sunset, the time at which they usually dig in for the night and become established at a site. Many adults flew away when they were released in the morning and afternoons. Transfer success was best with newly-emerged females.

The most successful and widely-used method is to transplant cores or blocks of soil containing prepupae. This must be done in spring (April) before the immatures transform into pupae or adults. Cores are placed on pallets and loaded on to a truck for transport. They should be covered with moist canvas or burlap if they are being trucked long distances. In this manner, several thousand cores can be moved by one semi-truck. When the cores arrive at a new site, they should be buried in 12 in (30 cm) trenches and puddled in with sparing amounts of water. Soil at the new site should be properly prepared before the transplants are installed. It should have about the same moisture content as the core. Cores should be installed in straight lines at least 4–6 in (10.2–15.2 cm) apart to ensure good soil moisture contact. They should never be stored for any length of time before burying them; this increases the risk of desiccation and decreases the viability of prepupae.

Managing the Lucerne Crop for Optimum Alkali Bee Pollination

Lucerne bloom should coincide with peak activity of alkali bee females if maximum seed production is to be realized. If necessary, bloom in commercial lucerne can be delayed in order to coincide with alkali bee activity, although this practice is seldom done now. Several methods can be used: harrowing, beating, spraying with dinitro material plus chlorpropham (Chloro IPC®), and clipping. If chemicals are used, they are applied about mid-April in early areas and in early May in later areas. Lucerne seed is considered a non-food crop for pesticide registrations in the northwestern US and parts of California. But certain chemical restrictions apply for lucerne used for animal feed. Cultivating can be done several times in late spring, depending on seasonal development. The grower may need to adjust timing programmes if early spring temperatures are higher than normal, a condition that stimulates alkali bees to emerge early.

Chapter 10

Other Soil Nesting Bees

Of the thousands of soil nesting bee species, only the North American alkali bees (*Nomia melanderi*) have been managed practically for crop pollination. Nevertheless, some other soil nesters are valuable pollinators where they occur naturally in significant numbers. Many bees in this group are extreme specialists which benefits the grower if this specialization happens to be for a crop. We concentrate in this chapter on soil nesting members of three bee families that have shown promise as pollinators in North America – the families Andrenidae and Apidae[1] (sometimes called *digger* or *miner* bees) and Colletidae (sometimes called *polyester* bees). A fourth family, the Halictidae, has a large and diverse number of species, but the most notable member of that group, the alkali bees, was covered in Chapter 9.

Biology

Soil nesting bees in North America tend to prefer sandy soils (Cane, 1991), but they also nest in silty soils (Miliczky *et al.*, 1990) and clay soils (Riddick, 1992). Some species prefer sunny banks of exposed earth along ditches while others nest in flat ground, with or without grass cover. Sometimes hundreds or even thousands of bees dig their tunnels close together, and their intense flight activity gives the false impression of a colony of social bees. Their subterranean nest design is some variation of a main tunnel with either terminal or side branches dead-ending into cells for developing young (Fig. 9.3). Soil nesters waterproof the earthen walls of cells with a glandular secretion. A mated female bee forages for pollen and nectar, provisions individual

[1]A recent revision (Roig-Alsina and Michener, 1993) places the former Anthophoridae within the Apidae, the same family as the social honey bees and bumble bees. Thus, the soil nesting apids we discuss in this chapter may be more familiar to readers as anthophorids.

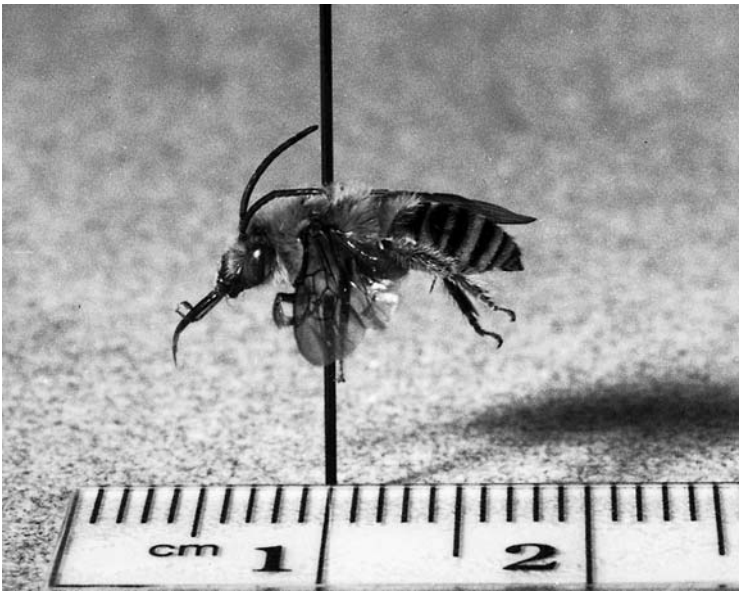


Fig. 10.1. The squash bee, *Peponapis pruinosa*. (Source: Nancy B. Evelyn.)

cells with food, and lays an egg in each cell, typical of the pattern for other solitary bees. Offspring tend to nest near the nest in which they were reared (Butler, 1965), which may explain why nesting areas remain active for years if they are left undisturbed.

Andrenidae

Bees in the family Andrenidae are slightly larger than worker honey bees. They dig their burrows in grassy areas or in bare soil. They often make aggregation areas of hundreds or thousands of nests, the largest recorded of which contained about 104,000 nests in a suburban backyard of 12,777 ft^2 (1187 m^2). Their nests have a mound around the entrance called a *tumulus*, a main vertical shaft 10–26 in (25–65 cm) deep, and 4–12 brood cells (Batra, 1984; Miliczky *et al.*, 1990; Riddick, 1992).

Apidae

Bees in the apid genus *Peponapis* are about the same size as honey bees (Fig. 10.1), and they are sometimes called squash or cucurbit bees because they only visit squash, pumpkin, or gourd. As such, they are

extremely effective pollinators of these crops. These bees make tunnels in high, well-drained bare soil and often under leaves, rocks, or other objects. Their nests have distinctive tumuli around the entrance, a main vertical shaft about 5–9 in (12–22 cm) deep, and 4–5 brood cells. Squash bees in the northeastern US overwinter as prepupae, pupate in late June or early July, and emerge in synchrony with cucurbit bloom. Nesting may continue until September, and individual females may make more than one nest per season. Large nest aggregations can recur in the same patch year after year if it is left undisturbed and surrounding fields are repeatedly planted in cucurbits (Mathewson, 1968).

Another apid, the southeastern blueberry bee (*Habropoda laboriosa*), is about the same size and colour as bumble bee workers (Fig. 10.2). Individuals of *H. laboriosa* emerge and mate, and females forage and nest in February–April in near-perfect synchrony with blueberry bloom in the southeastern US. Females dig nests in sandy soil 12–28 in (30–71 cm) deep. The bees avoid nesting in soils with deep clays, but some surface clays are tolerable. Nests may either be isolated or aggregated in groups. Sometimes the bees nest in soil that is hidden under thick layers of leaf litter and follow trails of small rodents under the litter in order to reach their nest entrances. The nest

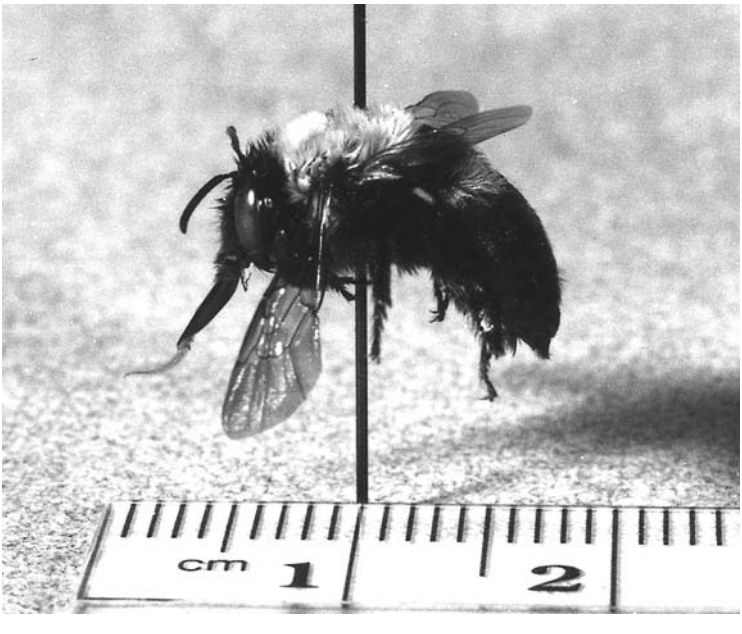


Fig. 10.2. The southeastern blueberry bee, *Habropoda laboriosa*. (Source: Nancy B. Evelyn.)

Fig. 10.3. A colletid, *Colletes* sp. (Source: Nancy B. Evelyn.)

is a vertical tunnel and usually contains two brood cells. Female *H. laboriosa* will provision cells with pollen from blueberry or sometimes oak. These bees appear to be near-obligate specialists on blueberry, and they are sometimes present in blueberry orchards in the southeastern US at economically important pollinating levels (Cane, 1993, 1994; Cane and Payne, 1988, 1991, 1993).

Anthophora pilipes villosula (sometimes called the 'shaggy fuzzyfoot bee') was introduced into the US from Japan in 1988. Females look like small bumble bees; males are smaller and grey coloured. The bees nest naturally in cliff faces, earthen banks, and adobe walls of human structures, and aggregations of nests are common. *A. pilipes villosula* begins emerging in Maryland in mid- to late March and remains active until early June. During that time territorial males mate with females, and newly-mated females dig one or more new nests or reuse old nests. Females dig simple burrows, line brood cells with a whitish-grey waxy substance, and provision each cell with a pollen–nectar mixture and an egg. Females may share a common entrance with a tunnel branching to each bee's separate brood (Batra, 1994).

Colletidae

Bees in the family Colletidae are called polyester or membrane bees because they waterproof their subterranean cells with a thin polyester lining which they excrete. They are about the same size and colour as honey bees (Fig. 10.3). Their nests have tumuli at the entrance, a vertical shaft 3–15 in (7–39 cm) deep, and 0–9 brood cells. Most nests are in bare soil, but they also occur in areas of thin grass (Batra, 1980).

Other Soil Nesting Bees as Pollinators

Andrenid bees have not been widely studied for their usefulness as crop pollinators, but they are relatively abundant and probably play an important role in some crops. Three species of *Andrena* (*A. carlini*, *A. carolina*, and *A. vicina*) are important pollinators of lowbush blueberry in Nova Scotia (Finnamore and Neary, 1978). *Andrena* species are the most abundant bee visitors in highbush blueberry (*Vaccinium corymbosum*) in New York, including the *Vaccinium* specialist *A. carolina* (MacKenzie and Eickwort, 1996). One *Andrena* species in western North America visits pear and probably is an effective pollinator when it occurs in large numbers, but it begins its active season too late to be a reliable pollinator for this crop (Miliczky *et al.*, 1990). However, since honey bees do not always work pear well, this supplemental foraging by *Andrena* may be important. Although honey bees are generally good pollinators of apple, they tend to rob flowers of 'Delicious' apple varieties. Some species of *Andrena* help compensate for this because they legitimately visit apple flowers (including 'Delicious'), specialize on apple, and work in cool temperatures (Parker *et al.*, 1987).

Squash bees (*Peponapis* spp.) outnumber all other bee species at squash blossoms at first morning light (Skinner, unpublished report) which coincides with the optimum time of day for pollinating squash (McGregor, 1976). Squash bees and honey bees pollinate cucurbits equally well, and there is no need to bring in supplemental honey bees if large numbers of squash bees are present (Tepedino, 1981).

Southeastern blueberry bees (*H. laboriosa*) are excellent pollinators of rabbiteye blueberry because they emerge from winter hibernation in time for early blueberry bloom, specialize on blueberry, buzz-pollinate the blossoms, and work very fast (Cane and Payne, 1988). They are more efficient than honey bees or bumble bee queens on a per-bee basis (Cane and Payne, 1990). However, the availability of southeastern blueberry bees varies across regions, and they are absent from up to 25% of cultivated blueberry orchards in the Southeast (Cane, 1993; Cane and Payne, 1993).

A. pilipes villosula has a relatively long active period in Maryland (March–June) which overlaps with spring-blooming apple and blueberry. It buzz-pollinates, forages in cool damp weather, and works from before dawn to after dusk (Batra, 1994). There is little experience with this bee in North America, but small-scale culturing methods are worked out (S.W.T. Batra, unpublished report). It seems to be a potential pollinator but it remains to be seen if it will become established widely in North America.

As for *Andrena*, bees in the genus *Colletes* have not been widely studied for their potential use as crop pollinators. They are capable of buzz-pollinating, and their active seasons (about 6 weeks) overlap spring blooming blueberry and cranberry (Batra, 1980, 1984; Parker *et al.*, 1987).

Conserving Wild Soil Nesting Bees

Chapter 4 covers bee conservation in more detail. Nevertheless, some points for conserving soil nesting bees bear repeating here.

The keys to large numbers of soil nesting bees are long-term undisturbed nest sites and dependable food sources. This was sadly demonstrated when a large recurring population of squash bees in Rhode Island, USA was decimated when its nest site was ploughed (Mathewson, 1968). Growers should seek out nesting areas of these bees and leave them as undisturbed bee sanctuaries. Even minor nest disturbances can be serious; southeastern blueberry bees have been known to abandon their nests if leaf litter at the entrance is moved (Cane, 1994). A dependable diet also is important. This is usually not a problem with more-or-less permanent blueberry orchards and their attendant populations of southeastern blueberry bees and *Colletes* species. However, it can be a problem with squash bees which depend on annual plantings of cucurbits. Continuous yearly plantings of cucurbits may be advisable to build up large recurring populations of squash bees, although other agronomic factors must be considered.

Relocating Soil Nesting Bees

Squash bees sometimes can be relocated by capturing adults with a net, chilling them (if a delay is necessary before release), and releasing them in squash fields that are in full bloom (Michelbacher *et al.*, 1971). The goal is to have bees nesting near the squash field. One should relocate large numbers of bees (hundreds, if possible) in order to compensate for the many that will immediately disperse from the field. It is helpful to release bees in early morning when squash nectar

is most abundant and attractive, or else in late evening when bees are less likely to fly.

Batra (1980) successfully relocated *Colletes* bees in Maryland by collecting copulating pairs, putting them in open-ended vials, and burying vials in a 2 × 16 ft (0.6 × 4.9 m) sand bed. The emerging females did not fly away but instead remained to make nests. Fruit growers could possibly boost numbers of *Colletes* or other soil nesters in their orchards with this method.

Chapter 11

Alfalfa Leafcutting Bees

The alfalfa leafcutting bee (*Megachile rotundata*, family Megachilidae) was accidently introduced to North America from Eurasia some time after the mid-1930s. Today it occupies the northern 75% of the contiguous US and extends from British Columbia to the Great Lakes region of Canada. It has become the major pollinator of seed lucerne in the western US and Canada. The bee is also managed as a lucerne pollinator in Europe, New Zealand, South Australia, and parts of South America.

Biology

The alfalfa leafcutting bee is a solitary bee that nests in pre-existing holes in wood or other materials. The bees are from $\frac{1}{5}$ to $\frac{2}{5}$ in (0.5–1 cm) long and $\frac{1}{12}$ to $\frac{1}{6}$ in (0.2–0.4 cm) wide (Fig. 11.1). Females are larger than males and are black with short white hair on various parts of the body. The abdomen of the female is more pointed than that of the male and has four or five stripes of white hair across the top and a pollen-carrying brush of long white bristles on the underside called the *scopa*. Males have buff-coloured hair, two light spots on the rear end, and lack the pollen brush. The male bee has mandibles with a prominent tooth that helps him cut through the leaf plug that seals his cell. The female's mandibles have smaller teeth well suited for cutting pieces of leaf that the female uses to line her cells.

Cells are made back to back in the nest tunnel (Fig. 11.2). The mother usually lays female eggs in the innermost cells and male eggs in the outermost. This arrangement, common to many solitary bees, enables the early-emerging males to chew out of their cells and leave the tunnel without damaging female cells. Adults emerge from cells in late spring or early summer, depending on temperature. Developing bees need a chilling period to break diapause. In the northwestern US,

Fig. 11.1. Alfalfa leafcutting bee, *Megachile rotundata*. (Source: Karen Strickler.)

depending on location and weather, males emerge from early to mid-June and females a week later. Males usually outnumber females two to one, but a one to one or even higher ratio of females sometimes occurs.

Females wait to mate until their second or third day post-emergence after which they start building cells. Males cluster in nests or other cavities at night, and their numbers dwindle after the females begin nesting. Females spend the night in the nest facing inward. They turn and face the entrance as temperatures rise in the morning, but they do not fly until temperatures exceed 70°F (21°C).

A female makes a thimble-shaped cell out of leaf pieces which she cuts, carries, and shapes by chewing their edges and pushing them against the wall of the tunnel. It takes about 15 leaf pieces to make one cell (Gerber and Klostermeyer, 1972), and each female makes 400–600 leaf collecting trips in her lifetime (Fairey and Lefkovitch, 1994). Fortunately, the benefit of these bees in lucerne seed production far exceeds the negligible damage caused by their foraging for leaf material.

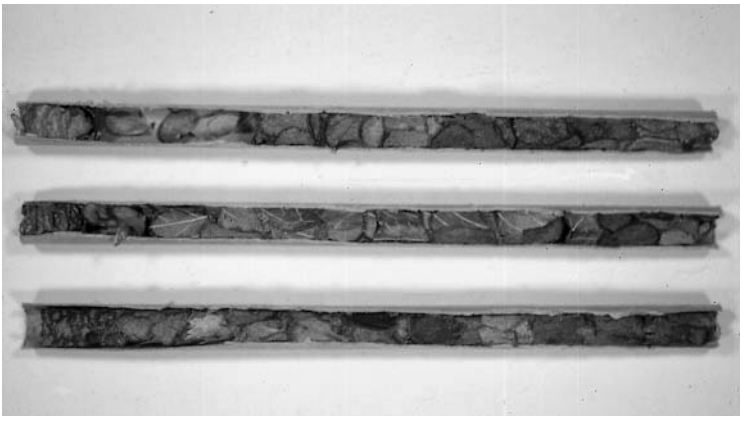
After a cell is formed, the female gathers nectar and pollen as food for the larva. The average provision mass is 64% nectar and 36% pollen. The female lays an egg on the surface of the nectar–pollen mass and caps the cell with round leaf pieces which form the base of the next cell. She makes, provisions, and lays eggs in successive cells until the tunnel is nearly full. Lastly, she makes a $\frac{1}{4}$ in (0.6 cm) entrance plug out of round leaf pieces. A female builds on average four to seven cells in a tunnel before she plugs it and repeats her labours in another tunnel. A female can finish about one cell per day during good weather. Females may take over nests from other females.

About 3–5% of all nests contain progeny of more than one female (McCorquodale and Owen, 1994).

Males live for 3–4 weeks. Females can live for 5–6 weeks but probably less than 4 weeks under field conditions. A female makes about 28 cells in her lifetime under controlled conditions, but 16 is a good average in nature. The number of nesting females usually drops sharply 6–7 weeks after their emergence.

The leafcutting bee has two emergence periods each year in the northwestern US and Nevada. Generally, 10–20% of the brood emerge the same season as their parents; these are called second- or summer-generation adults.

(a)



(b)

Fig. 11.2. (a) Three nest straws of the alfalfa leafcutting bee showing the back-to-back arrangement of cells. (b) Cells that have been partially opened to reveal the prepupae within. (Source: Karen Strickler.)

Alfalfa Leafcutting Bees as Pollinators

The alfalfa leafcutting bee has distinguished itself as an efficient and practical pollinator of lucerne. Each female can trip enough flowers to produce up to $\frac{1}{4}$ lb (0.1 kg) of seed. It can nest in many kinds of artificial and natural cavities and be propagated under a wide range of climatic conditions. The range of alkali bees, on the other hand, is limited by their requirement for very particular soil types.

Leafcutting bees made lucerne production possible in areas of western North America where it could not previously be grown economically. For example, Canada was importing lucerne seed in 1950 to meet domestic demand, but by 1988 western Canada was exporting 2.4 million lb (1.1 million kg) of seed (Richards, 1993). This dramatic turnaround was fuelled in part by the successful use of alfalfa leafcutting bees. In the northwestern US, about 2.2 billion leafcutting bees, valued at US$10.9 million, were used to pollinate lucerne in 1990 (Peterson *et al.*, 1992).

Bohart (1972) reviewed some of the advantages of the alfalfa leafcutting bee as a pollinator:

- It collects lucerne pollen readily and efficiently trips the lucerne flower.
- It forages in the field where it nests. Therefore, it is less likely to visit other crops or be killed by insecticides on neighbouring fields.
- Its foraging period generally coincides with the blooming period of lucerne.
- It emerges readily and predictably after a controlled period of cold treatment followed by incubation.
- It has a long foraging life (4–6 weeks) compared to other solitary bees and produces a large number of offspring.
- It nests in large groups or aggregations which simplifies its management and increases its effectiveness as a pollinator.
- It readily nests above ground in artificial nests.
- Because its leaf cells are tough, overwintering larvae can be handled with bulk labour-saving methods.

The leafcutting bee is a promising pollinator for other crops beside lucerne. Average seed yield of red clover in northern Alberta was 366 lb acre^{-1} (410 kg ha^{-1}) when leafcutting bees were used as pollinators, but only 260 lb acre^{-1} (291 kg ha^{-1}) when they were not used. Moreover, the bees reproduced on red clover nearly as well as on lucerne (Fairey *et al.*, 1989). Leafcutting bees improved fruit set by up to 30% over the background pollination provided by honey bees and native bees in lowbush blueberry in Maine (Stubbs and Drummond, 1997). Richards (1991) ranked leafcutting bees as ‘very

good' pollinators of Canadian alsike clover ('Dawn'), birdsfoot trefoil ('Cree'), cicer milkvetch ('Oxley'), crown vetch ('Penngift'), red clover ('Norlac', 'Ottawa'), sainfoin ('Nova'), white clover, white sweet clover, and yellow sweet clover.

In contrast, leafcutting bees do not always exhibit desirable pollination behaviours nor performance. Although they visit lowbush blueberry in Maine at comparatively low temperatures between 56 and 73°F (13.5–23°C), they also are distracted by nearby non-crop plants (Stubbs *et al.*, 1994). The bees are, in fact, moderately catholic in taste and known to visit flowers of 21 species of plants representing 14 genera and seven families (Small *et al.*, 1997), a habit that can compromise their fidelity to a particular crop. Leafcutting bees visit apple blossoms in Washington, but they tend to fly only when temperatures exceed 75°F (24°C) (D.F. Mayer, unpublished data); moreover, it is difficult to synchronize bee incubation and emergence with apple bloom (see page 113). Kiwifruit flowers are not attractive to leafcutting bees, so it is unlikely that they will be effective pollinators for this crop (Donovan and Read, 1988). Cage studies with winter vetch and hairy vetch failed to demonstrate effective pollination by leafcutting bees (Richards, 1997).

Recommended Bee Densities

The recommended leafcutting bee densities for lucerne in the US have tended to increase over the years. A range of 5000–10,000 female bees acre^{-1} (12,350–24,700 females ha^{-1}) was once recommended, but 14,000 females acre^{-1} (35,000 females ha^{-1}) is now typical (Baird and Bitner, 1991). Some growers in Idaho introduce over 21,000 females acre^{-1} (52,000 females ha^{-1}) (Strickler and Freitas, 1999). Recommended densities tend to be a little smaller in Canada, about 7000 females acre^{-1} (17,500 females ha^{-1}) (Fairey *et al.*, 1984). Seven thousand females can set a 1 acre (0.4 ha) field in 10–14 days under ideal conditions.

Extremely high bee densities may contribute to a reduction in bee yield in modern alfalfa leafcutting bee culturing systems. As bee densities have increased in recent years, so have problems with larval mortality (Mayer, 1993), owing perhaps to competition for resources and disorientation by females at nests. Growers favour high bee densities because they result in rapid pollination. Computer simulation models suggest that there is indeed an advantage to high bee densities in that pollination is completed more rapidly the more bees are introduced (Strickler, 1996, 1997). However, high bee densities also are associated with a rapid depletion of floral resources (within 3–4 weeks) which may negatively impact bee populations

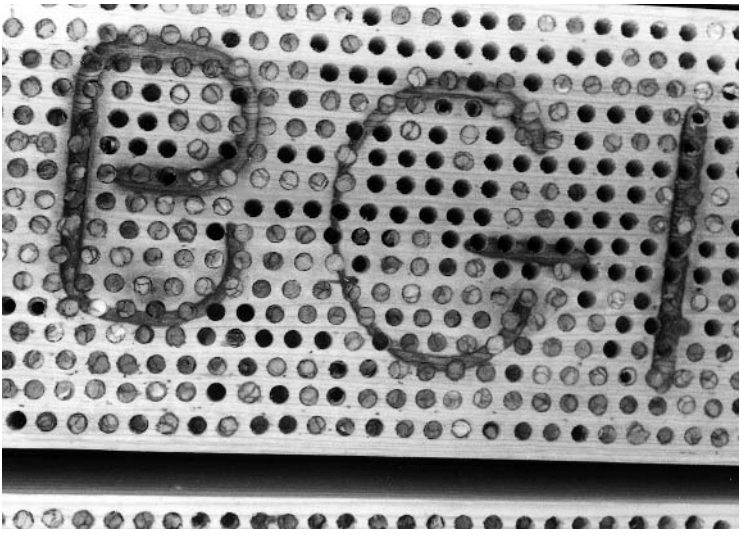


Fig. 11.3. Solid nesting board for alfalfa leafcutting bees. (Source: Daniel F. Mayer.)

(Strickler and Freitas, 1999). Thus, there may be a trade-off at work in this bee–lucerne propagation system in which the grower must compromise the speed with which the crop is pollinated with the desired increase in bee numbers (Stephen, 1981).

Rearing and Managing Alfalfa Leafcutting Bees

Alfalfa leafcutting bees readily accept artificial nesting tunnels made from a variety of materials. Taking advantage of this behaviour, growers and researchers have developed practical methods for mass-rearing leafcutting bees. Management is based upon providing nesting holes and shelters in seed fields, protecting bees during their dormancy, and activating dormant bees in time to pollinate the crop. Appendix 1 includes a list of vendors that sell leafcutting bees and rearing supplies.

Nesting materials and shelters

Bees must be provided nesting materials and some kind of artificial tunnel in which to nest. Nesting materials and the bees must, in turn, be provided a field shelter to protect bees from weather and provide them an orientation landmark while they provision their nests.

Here follows a summary of some of the most common nesting materials (Peterson *et al.*, 1992):

- Solid board (Fig. 11.3) – a solid wooden board, $47\frac{1}{4} \times 6 \times 2\frac{3}{4}$ in ($120 \times 15 \times 7$ cm), with ~2000 drilled holes per board, each hole $\frac{7}{32}$ in diameter and $2\frac{5}{8}$ in deep (5 mm diameter × 65 mm deep) (see page 113).
- Removable-back solid board – similar to above except the back can be removed to punch out cells (see page 115).
- Laminated grooved board (Fig. 11.4) – a pair of wood or plastic boards with opposing grooves that form tunnels when strapped together. These nests can be taken apart to remove cells and sanitize the boards (see page 115).
- Polystyrene nest board (Fig. 11.4) – similar to laminated grooved boards, but lighter and less expensive (see page 115).
- Paper nest board – like laminates or polystyrene nest boards, but designed to be used only once.

Nesting materials and bees must be housed in proper field shelters to ensure good bee activity and propagation. Most shelters have three sides, a roof, and a floor (Fig. 11.5), but designs are variable and include modified tractor trailers and school buses. The roof should have a 12–18 in (30–46 cm) overhang to protect nest boards from direct sunlight. Some growers use an awning to further protect nest boards from sun. There should be a 4–6 in (10–15 cm) gap between

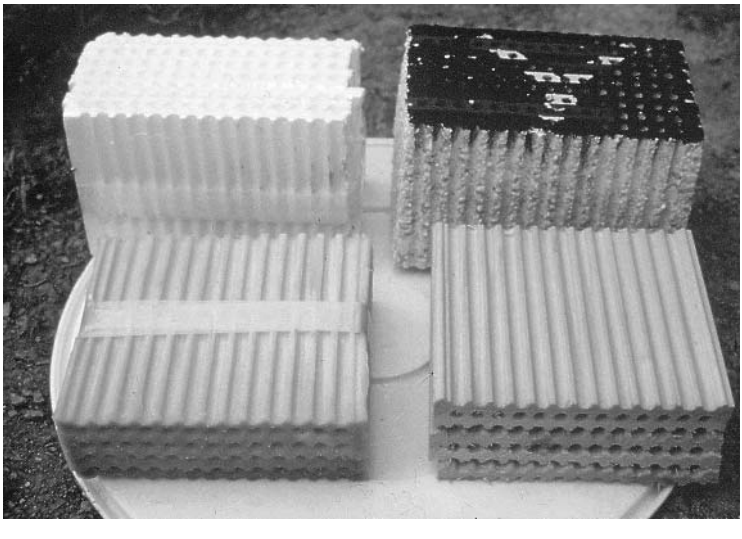


Fig. 11.4. White polystyrene laminate nesting boards (rear left), polystyrene block (rear right), wood laminate nesting boards (front). (Source: Rhéal Lafrenière.)

Fig. 11.5. Field shelter for alfalfa leafcutting bee nesting boards. (Source: Rhéal Lafrenière.)

the top of the sides and the roof to let hot air escape from inside the shelter. Shelters should be painted yellow, blue, or green and marked with various geometric symbols to help bees orientate to the shelter (Richards, 1996). Bees orientate best to large objects in a field and work most efficiently when they are housed in large shelters; Stephen (1981) recommends shelters 20 ft long and 10 ft high (6 × 3 m). It is convenient to build shelters on trailers so that they can be moved to other late-blooming fields or away from insecticide applications. If there is a problem with birds preying on bees, the fronts of shelters can be covered with a 2 in (5 cm) mesh wire screen. A smaller mesh size may injure the bees as they fly through the screen.

Shelters should be large enough to accommodate at least 60,000–80,000 nest holes (Stephen, 1981). Shelters with 30,000–90,000 holes can provide enough female bees for 2–6 acres of seed (0.8–2.4 ha), but their small size increases the tendency for bees to drift, especially if there are larger shelters nearby. Large shelters with 150,000–750,000 nesting holes can provide for 10–50 acres (4–20 ha), but they are costly to build and may increase problems with bee parasites and diseases.

Nest boards are placed inside the shelter, stacked back-to-back in rows. There should be at least 24 in (60 cm) between facing nest boards; leafcutting bees must be able to fly freely within the shelter. The faces of nest boards are painted with various shapes and symbols about 4 in (10 cm) in diameter to help bees orientate to their own particular nest holes. Nest boards should not touch the shelter's siding or ceiling as these surfaces tend to get very hot.

Shelters in most regions should face slightly north of east so that the nests are not in direct sunlight after 10 a.m. Some growers attach an awning to the front of the shelter so it can be faced south or southeast to increase interior ventilation by prevailing winds. Small shelters should not be placed next to large, trailer-size shelters because the bees tend to drift to the larger shelters.

Cold storage and incubation

Cells of immature leafcutting bees should be kept in cold storage for most of the year and then carefully incubated to bring about bee emergence in time for the crop bloom.

Nesting materials should be removed from fields in mid-August to September and held at ambient temperatures for 2–3 weeks. This gives the bee larvae time to moult into prepupae and spin cocoons. Cocoons are then stored at 41°F (5°C) and 40–60% relative humidity until the following spring.

In spring, the cells are switched from cold storage to incubation at 86°F (30°C); this process must begin about 21 days before the anticipated beginning of crop bloom. If the weather turns cool and crop bloom is delayed, the emergence of bees can be delayed by lowering the incubation temperature to 59–68°F (15–20°C) during the 15th to 19th day of incubation (Rank and Goerzen, 1982). Bees are then put in field shelters, and it is important to do this only on warm, still days. If the temperature is cold the bees will be sluggish and birds may eat them, and if it is windy the bees will have trouble orientating to their nests.

Solid wood/phaseout rearing system

This is the most common method used in the western US. Diapausing larvae are kept in their solid wood nest boards during cold storage, and nest boards can be reused over and over (see 111). The biggest disadvantage is that reused nesting material can accumulate diseased spores and insect enemies over time. Hence, old nest boards should be *phased out* every other year; this happens when bees are returned to field shelters at the start of crop bloom.

To phase out old boards, the boards are first switched from cold storage into incubation 21 days before bloom as usual. When the boards are taken to the field, they are placed in *phaseout boxes* next to the field shelters. A phaseout box can be any kind of large enclosure (a tractor trailer works well) with numerous slits ~2 × 6 in (5 × 15 cm) in the walls. The field shelters are fitted out with newly-sanitized, empty nest boards. As bees emerge from their nest boards in

the phaseout box, they are attracted to light, fly out through the slits, and begin nesting in the clean boards in the nearby shelter. The old nest boards are then reamed out with a mechanical corkscrew device to remove nest debris. Boards are then sanitized either by kilning them at 260–300°F (127–149°C) for 24 h (Stephen, 1982), by dipping them in calcium hypochlorite (bleach) (Mayer *et al.*, 1988a), or by fumigating them with paraformaldehyde (Mayer *et al.*, 1991).

Boards full of bees but not yet scheduled for phaseout are placed directly in the field shelters from incubation. The grower must provide 1–1½ empty sanitized boards in the shelter for every full board to allow for population expansion.

Because polystyrene or paper nest boards are inexpensive (see page 111), many growers use them in phaseout systems as they would solid wood nest boards. However, polystyrene or paper boards were designed for loose-cell systems, and bee emergence is delayed when they are incubated in these nest materials. Therefore, polystyrene or paper nests are not advisable for phaseout systems (Peterson *et al.*, 1994).

Fig. 11.6. Loose cells are incubated in enclosed screen trays. (Source: Daniel F. Mayer.)

Loose-cell rearing system

Cells are removed from nest boards with this system and stored and incubated loosely in trays. Emerged bees or mature cells are released in field shelters in spring and provided with clean, empty nest boards for nesting. This method allows for better control of bee parasites and nest destroyers, reduces space needs during cold storage, and reduces spread of disease. However, it is labour intensive.

The loose-cell method requires a removable-back solid nest board or a grooved laminate board (see page 111). The nest boards are opened and the cells punched or stripped out after the larvae have moulted to prepupae at the end of the nesting season. Cells are then sifted through a screened tumbler in order to remove loose leaf pieces, chalkbrood-infected cells, and many of the insect enemies. Cells are put in large, covered containers and placed in cold storage.

In spring the loose cells are incubated in enclosed screen trays (Fig. 11.6) at 86°F (30°C). Each tray is 2 × 2 or 2 × 3 ft (61 × 61 or 61 × 91 cm) and holds about 2 gal (7.6 l) of cells. Incubation rooms can be fitted with 'bread racks' to hold large numbers of trays. There should be about $1\frac{1}{2}$ in (3.8 cm) between trays to allow for air circulation. It is important to maintain temperatures carefully because loose cells are more vulnerable to temperature extremes than are cells insulated in nest boards. By days 21–24 the first males, and maybe some females, are starting to emerge and the trays are ready to go to the field shelters.

But first, one must determine how many gallons of bees to put in each field shelter. One gallon (3.8 l) holds about 10,500 leafcutting bee cells, one-third of which will contain females (3465 females gal^{-1}; 915 females l^{-1}). There need to be about three vacant nest holes for every female bee (it is not necessary to provide nest holes for males). Using the formulae below, we find that a shelter that holds 80,000 nest holes (~40 boards of 2000 holes each) can accommodate ~8 gal or 30 l of cells. This equates to about four trays. So, a good guideline is to provide five empty nest boards per gallon of cells (1.3 boards per litre of cells).

$$\textit{Required gallons of cells} = \frac{\textit{no. holes per shelter}}{3} \div 3465$$

or

$$\textit{Required litres of cells} = \frac{\textit{no. holes per shelter}}{3} \div 915$$

The 80,000-hole shelter we used in the example with ~27,720 females (8 gal of cells × 3465 females gal^{-1}) and a lower target population of 5000 females $acre^{-1}$ (see page 109) is good for pollinating about 5 acres.

Before trays and empty nest boards are put in the field shelters, the empty nest boards must be sanitized by kilning them at 260–300°F (127–149°C) for 24 h. It is also a good idea to spray the field shelters with a 3–6% hypochlorite (bleach) solution to help control chalkbrood disease. Trays are placed inside shelters in the shade, and the bees are released by removing the top screen. Bees will mate and females will begin nesting in the nest boards, and trays will be empty of live bees within a week or so. If the nesting rate is high the grower may need to add more nest boards to the shelter. It may be necessary to move the shelter to another blooming field if the field finishes blooming before the last bee cells are provisioned.

Shelter Placement in the Field

Alfalfa leafcutting bees prefer to forage within ~300 ft (100 m) of their nest (Free, 1993). Therefore, in large fields it is important to place shelters inside the field as well as along the edges to get good bee coverage.

Enemies and Diseases of Leafcutting Bees

There are over 20 species of insect parasites, predators, or nest destroyers of leafcutting bees (Peterson *et al.*, 1992). Parasitoids in the genera *Melittobia*, *Monodontomerus*, *Pteromalus*, and *Tetrastichus* typically become active and emerge before the bees on days 8–13 of incubation. They are especially serious in loose-cell systems because the autumn tumbling process does not eliminate them (they are protected inside parasitized cocoons), and the exposed cells during spring incubation are easy targets. Parasitoids can be controlled with one or more of the following methods:

- Placing an ultraviolet light over a pan of soapy water on the floor of the incubator. Parasitoids are attracted to the light, fall in the water, and drown.
- Covering cells in the trays with a 1 in (2.5 cm) layer of clean, dry sawdust.
- Lightly spraying loose cells with DEET or a similar approved insect repellent.
- Treating the incubator with dichlorvos resin strips (Vapona®) or a similar approved insecticide between days 8 and 13, followed by

24 h of active ventilation. Autumn treatments of dichlorvos for up to 7 days also may be helpful (Goerzen and Murrell, 1992).

Many nest destroyers are removed in loose-cell systems during the autumn tumbling procedure. With solid board/phaseout systems, the phaseout box exit slits can be fitted with special excluders that let the bees escape but trap certain nest destroyers such as chequered beetles. With either system, one can trap nest-destroying beetles at the field shelters with yellow Japanese beetle traps containing Vapona® strips.

The most serious disease problem is chalkbrood, a fungus that attacks and kills leafcutting bee larvae. The fungus is similar to the chalkbrood fungus affecting honey bees, but the two are different species and only affect their respective bee hosts. In leafcutting bees, the chalkbrood-infected larvae become hardened and appear chalky, grey, or black. Chalkbrood disease can be limited with one or more of the following practices:

- With solid board systems, it is important to phase out used boards every other year. Boards must be reamed out and sanitized with heat, a 3% hypochlorite (bleach) solution, or with paraformaldehyde fumigation.
- With loose-cell systems, the cells must be tumbled in autumn to sort out and remove chalkbrood cells. If disease is present it is advisable to dip healthy cells in a 1–3% bleach solution and let them dry. Used nest boards must be sanitized.
- With either rearing method, it is a good practice to spray field shelters with a 3–6% bleach solution before adding new boards and bees.

Although growers are interested in using fungicides for chalkbrood control, it is unlikely that such products will be approved in the US in the near future. Only one fungicide has been approved for use in leafcutting bees in North America – paraformaldehyde by the government of Canada. Paraformaldehyde fumigation effectively kills chalkbrood spores in rearing equipment within a temperature range of 68–90°F (20–32°C) and humidities above 60% (Mayer *et al.*, 1991, Goettel *et al.*, 1993). Paraformaldehyde fumigation is relatively easy compared to other chalkbrood-sanitizing measures such as heat or bleach dip.

Chapter 12

Orchard Mason Bees

Biology

Bees in the genus *Osmia* (family Megachilidae) have proven themselves to be effective pollinators of apples and other orchard fruits. These solitary bees nest in hollow reeds or pre-existing holes in wood such as abandoned beetle burrows or nail holes. They may nest in large aggregations if nest holes are abundant. *Osmia* bees partition cells and seal their nests with mud, chewed leaf material, or a mixture of both – hence, they are sometimes called *orchard mason bees*.

The most important member of this group in North America is the native blue orchard bee, *Osmia lignaria*. The eastern subspecies (*O. lignaria lignaria*) occurs from the eastern slopes of the Rocky Mountains to the Atlantic. The western subspecies (*O. lignaria propinqua*) occurs from the western slopes of the Rockies to the Pacific Ocean. Females of the blue orchard bee have a pair of horn-like projections extending from the lower face. The blue orchard bee is shiny blue/black and about two-thirds the size of a honey bee (Fig. 12.1). The male is about a third smaller than the female and has a white patch of hair on the face and long curved antennae. Females have no white on the face and their antennae are about half as long as those of males.

The horned-face bee (*O. cornifrons*) was introduced from Japan into Utah in the 1960s, and from Utah to Maryland by 1978 (Batra, 1989); it has since become established in many areas of the eastern US and Canada. It has a pair of horn-like projections on the lower face.

The orange orchard bee (*O. cornuta*) was introduced from Spain to California almond orchards in the 1980s (Torchio, 1987). The female is slightly larger than the female blue orchard bee. Its most distinguishing characteristic is an abdomen coated with beautiful, bright orange hair. It also has a pair of horns on the lower face.

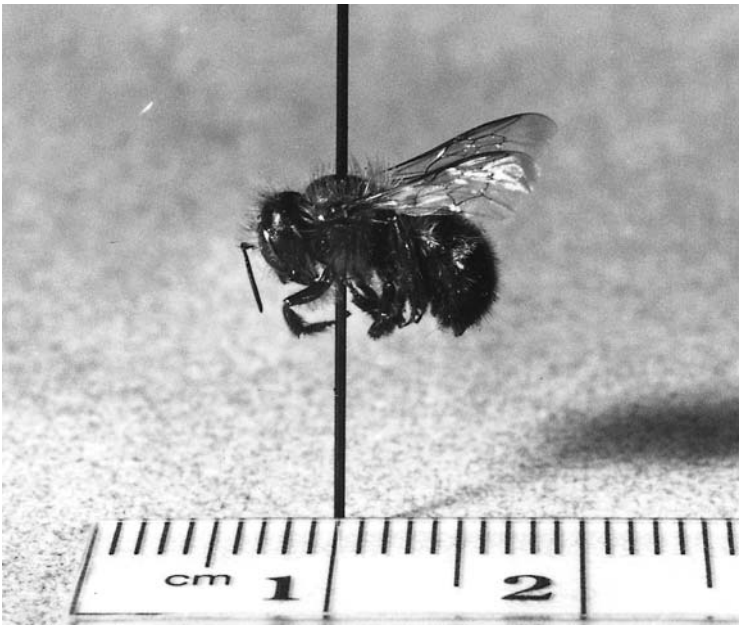


Fig. 12.1. The blue orchard bee, *Osmia lignaria*. (Source: Nancy B. Evelyn.)

O. ribifloris biedermannii is a metallic green or blue-coloured mason bee native to areas of the western and southwestern US. It is a potential pollinator of highbush blueberry (Torchio, 1990b).

Male and female orchard mason bees emerge from nests and mate in spring when temperatures exceed 50°F (10°C). Males emerge 3–4 days earlier than females and patrol nesting sites looking for females. Males will forage at flowers for nectar but accomplish little pollination. When a new female emerges, a waiting male pounces on her to mate. A female may mate with several males.

The female finds a suitable nest tunnel and begins making cells in the back-to-back pattern typical of most solitary bees. Usually only one female nests in a given hole. Females do not forage for cell provisions unless temperatures exceed 55°F (12.8°C). The female collects nectar and pollen and makes a pollen mass in each cell. *Osmia* species carry pollen with an abdominal scopa. It takes 11–35 foraging trips to collect enough pollen and nectar for one cell. The female lays an egg, $\frac{1}{8}$ in (3 mm) long and sausage-shaped, with one end embedded in the pollen mass. After the female lays the egg, she partitions the cell from others with a thin wall of mud or chewed leaf material. Each partition takes 8–12 mud-collecting trips, and a female usually completes one cell per day. Female eggs are laid in cells towards the bottom of the tunnel and males are produced near the

entrance; the average sex ratio is two-thirds male. After she fills the nest tunnel with cells, the female covers the entrance with a thick mud cap.

All stages of development occur between 59 and 86°F (15–30°C). Eggs hatch at about day seven. The larva eats pollen for about 30 days and then defaecates. It rests for several days then starts to spin a pinkish-white silk cocoon around itself, weaving faecal pellets into the cocoon's outer layer. In a few days the cocoon turns a dark brown colour, and after about 30 more days the larva pupates. After two weeks the pupa moults into an adult. It is these new adults that overwinter in dormancy. Temperatures in winter must be lower than 40°F (4.4°C) or adults will not be able to break dormancy and emerge in spring. Adult females provision cells and pollinate for 4–6 weeks and then die. There is only one generation per year.

Orchard Mason Bees as Pollinators

Osmia are used for commercial crop pollination in some parts of the temperate world, most notably Japan where native *O. cornifrons* is used to pollinate orchard crops. Mason bee management in North America has not progressed much beyond the experimental or hobbyist stage in spite of research evidence that they are efficient pollinators. Early-stage studies typically measure pollinator potential by observing bee reproduction. If bees can rear a brood with the pollen and nectar from a particular crop, then the potential for pollination is there. Introductions of exotic *Osmia* into North America have met with mixed success, and commercial-scale production like that of honey bees, alkali bees, and leafcutting bees is not worked out. One recurring problem is the high number of females that disperse away from the orchard when they are released in spring. Nevertheless, these bees are good pollinators where they occur in large numbers, whether as natural or introduced populations.

Blue orchard bees (*O. lignaria propinqua*), when introduced into California almond orchards, collect almond pollen, occupy man-made nests, and increase in population size, all of which indicates that they are potential pollinators for this crop (Torchio, 1981a,b). However, over 50% of females disperse away from the release site before nesting when they are released in February (Torchio, 1982). Orange orchard bees (*O. cornuta*) were introduced into California almond from Spain in 1984; the bees overwintered in commercial orchards, emerged in synchrony with almond bloom, nested gregariously in man-made nests, landed directly on the sexual parts of the flowers, collected almond pollen, and the immatures developed normally on provisions of almond pollen and nectar (Torchio *et al.*, 1987). But, as with blue

orchard bees, many females dispersed away from the orchard before nesting. It may be possible to minimize spring dispersal by releasing bees in their natal nests rather than by mass-releasing them in adult emergence boxes (Bosch, 1994a). Overall, efforts to develop almond pollination with orange orchard bees seem justified; each *O. cornuta* female visits 9500–23,600 almond flowers during a season, and only three females per tree are needed to achieve maximum pollination (Bosch, 1994b).

Blue orchard bees (*O. lignaria lignaria* and *O. lignaria propinqua*) are efficient pollinators of apple because they land directly on the anthers and stigma of the blossom, thus maximizing the chance of successful pollination (Torchio, 1985). Honey bees, on the other hand, sometimes rob an apple flower of its nectar without pollinating it; this happens most often with the 'Delicious' apple variety. In North Carolina orchards of 'Delicious' apples in which *O. lignaria lignaria*, *O. lignaria propinqua*, and *O. cornifrons* were experimentally released, fruit-set was higher in areas near *Osmia* nests than in areas without *Osmia* nests, even if those areas had honey bee hives. Apples grown from areas near *Osmia* nests had comparatively more seeds and better fruit shape (Kuhn and Ambrose, 1984). However, these introduced populations of *Osmia* did not establish well in the test orchards, so the long-term benefit of these introductions was doubtful. The authors blamed this on pesticides, rain, dispersal of adults away from the site, and high mortality of immature bees from unknown causes. In a Japanese apple orchard with honey bees and horned-face bees, the horned-face bees visited more apple flowers per minute (15) than did honey bees (8.5), and in 15 min made more contact with the sexual column of flowers (105 contacts versus 4) (Batra, 1982). *O. cornuta* prefers almond pollen but will switch to apple if it is more readily available (Márquez *et al.*, 1994).

O. ribifloris are efficient pollinators when they are released in California highbush blueberry orchards (Torchio, 1990b). The female is fast-flying, and it takes at least 11 foraging trips to provision one brood cell. The bees visit flowers legitimately, working the flower with the front legs to release pollen (*O. ribifloris* does not buzz-pollinate blueberry although males 'buzz' during courtship). An *O. ribifloris* female spends about three seconds at each blueberry flower, and the bee's head morphology ensures pollen transfer between blueberry plants. In the California study, the introduced bees provisioned cells with blueberry pollen exclusively and the immatures developed normally. *O. ribifloris* females do not disperse away from the orchard as readily as do other *Osmia* species. The bees nest in man-made structures. Field-trapped bees can be overwintered and transported, and their emergence can be synchronized with blueberry bloom. The California study was not without problems.

Death rate of immatures was high at one site and the population declined. Parasitism was high during 2 years, and male production ranged from 2.2 to 4.6 males per female (males are comparatively inferior pollinators). Nevertheless, *O. ribifloris* seems to be a good candidate for commercial pollination in highbush blueberry.

Osmia bees are promising candidates for lowbush blueberry pollination. Adult emergence in Maine is well synchronized with crop bloom, and the bees forage in a wide range of temperatures, provision nests exclusively with blueberry pollen, and successfully overwinter in the field (Stubbs *et al.*, 1994). Wild populations of *O. atriventris*, *O. inspergens*, and *O. tersula* are known visitors of lowbush blueberry in Québec, but they are probably minor pollinators (Morrissette *et al.*, 1985). *O. inermis* and *O. proxima* in Nova Scotia collect lowbush blueberry pollen to provision their cells (Finnamore and Neary, 1978).

Overall, *O. cornifrons* and *O. lignaria propinqua* have not been satisfactory pollinators of orchard crops in Washington (D.F. Mayer, unpublished data). Reproduction of spring-introduced bees in cherry and pear ranged from 10 to 50%, and bees were rarely seen visiting cherry or pear flowers. Females apparently foraged on many non-crop flowers and dispersed away from the orchards.

Recommended Bee Densities

For almond, Bosch (1994b) recommends three *O. cornuta* females per tree. For apple, as few as 250 nesting *O. lignaria propinqua* can pollinate 1 acre of apple (618 bees for 1 ha) (Torchio, 1985). For a variety of orchard fruits, Batra (1982) recommends 2834 *O. cornifrons* acre^{-1} (7000 ha^{-1}). For highbush blueberry, Torchio (1990b) recommends 300 nesting female *O. ribifloris* acre^{-1} (741 ha^{-1}).

Rearing and Managing Orchard Mason Bees

Orchard mason bees readily nest in man-made nesting materials such as smooth holes drilled in solid blocks of wood, hollow natural reeds, and cardboard tubes (Griffin, 1993; S.W.T. Batra, unpublished report). Regardless of the nesting material used, nest holes should be $\frac{5}{16}$–$\frac{3}{8}$ in (8–10 mm) in diameter and about 6 inches (15.2 cm) deep. Nest hole diameters smaller than $\frac{5}{16}$ in will encourage high production of males which are comparatively poor pollinators.

Cardboard tubes are especially suitable because they are relatively inexpensive, disposable, and thick enough to discourage entry of many parasites (Fig. 12.2). Paper soda straws are easily penetrated by

nest enemies, and plastic soda straws retain too much moisture. Cardboard tubes are available from local paper supply companies or from vendors listed in Appendix 1.

Nest materials must be housed in some kind of weather shelter. It is possible to make an adequate shelter by stretching a tarp over a frame or by using a lean-to, clean empty drums, garbage cans, or overhanging eaves of buildings. Shelters must shield bee nests from rain and direct afternoon sun. The shelter opening and nest entrances should face east, south, or southeast so that the morning sun can warm bee nests and stimulate early flight. Shelters must be ventilated to prevent excess heat build-up. They should be painted a light colour, but not in a bright metallic finish because the shine may repel bees. It is a good idea to cover shelter entrances with bird netting or with $1\frac{1}{2}$–2 in (3.8–5.1 cm) chicken mesh in order to repel birds, racoons, or other animals that may attack the nests. Bird netting is the preferred material because chicken wire can damage bees' wings.

A horizontal section of white 3 in (7.6 cm) polyvinyl chloride (PVC) pipe makes a good shelter for bees nesting in cardboard tubes. One end of the PVC pipe can be cut at a 45° angle so that the top sticks out past the bottom and acts as a rain shield. The other end is closed with a plastic cap. The bottom part of the PVC pipe (the long run constituting the floor) must be at least 8 in (20.3 cm) long. One can then take standard $\frac{5}{16} \times 16$ in (0.8×40.6 cm) cardboard tubes, fold each in half to make two 8 in (20.3 cm) lengths (tunnels must dead-end or bees will not nest in them), and place a bundle of tubes

Fig. 12.2. Orchard mason bees will readily nest in cardboard tubes. Each tube is folded in half to produce two dead-end tunnels. (Source: Keith S. Delaplane.)

Fig. 12.3. A field shelter for orchard mason bees. A section of PVC pipe is filled with cardboard nesting tubes, each of which is folded in half to make two dead-end tunnels. The front of the PVC pipe can be cut to produce an overhang for rain protection, and the back should be sealed with a plastic cap. The shelter should be securely tied to fence posts or trees so that it does not sway in the wind. (Source: Keith S. Delaplane.)

horizontally inside the PVC pipe. In the orchard, each pipe full of cardboard tubes is securely fastened on to a tree or a stand at least $2\frac{1}{2}$ ft (0.8 m) off the ground (Fig. 12.3). Shelters must not be hung in such a way that they sway in the wind. There must be a source of mud at each site so that bees will have a ready supply of mud for making nest partitions.

If the objective is to encourage and augment existing natural populations of orchard mason bees, one simply needs to put out shelters full of empty nesting material in early spring as soon as bees become active. Chances are good that bees will nest in the shelters. If one is releasing dormant bees overwintered in nest tubes, the shelters must be placed in the orchard in early spring 3–7 days before crop bloom. If the weather turns cold and bloom is delayed, bee emergence can be delayed by putting the nest material full of bees in a refrigerator at 39–40°F (3.9–4.4°C). Bees must be removed from refrigeration 3–7 days before expected crop bloom. Adult males begin emerging shortly thereafter, and females begin emerging 2–3 days later. It is best not to move shelters once females start nesting. If they must be moved, it is preferable to move them at night and take them at least $\frac{1}{2}$ mile (0.8 km) away from the old location.

Nest materials full of developing bees should be removed from the orchard after nesting season and stored, protected from parasites and

nest enemies, in a cool, unheated, dark place. Dormant bees must experience some freezing temperatures before they can break dormancy in spring, and ambient winter temperatures will work adequately except in areas that experience cold spells below 5°F (−15°C). During these cold snaps, it is advisable to store bees in slightly warmer conditions at 10–40°F (−12.2–4.4°C). Some growers leave dormant bees outdoors in their shelters all winter. If this is practised, it is important to screen shelter entrances to exclude nest enemies.

Bee parasites may emerge from cells during storage. It may be possible to catch these parasites with a strip of flypaper hung near a window or other source of light. If mice are a problem the nest materials must be stored in mouse-proof screened boxes.

Bees will reuse old nest tunnels, but nest materials should be replaced every 2–3 years to avoid build-up of diseases and enemies. One way to phase out old nest material is to place it, full of bees, inside a black plastic bag. When bees are ready to be released in spring, the bag of old, occupied nest material is placed in the shade towards the rear of the shelter (this method works best with spacious shelters such as old drums). The mouth of the bag is reduced just enough to let air in and bees escape, and it is turned to face towards the shelter entrance. New, clean, empty nest material is placed in front of the old material and closer to the shelter entrance. When bees return to the shelter they tend to occupy the new nest holes, ignoring the old ones at the rear. The old nest material is then discarded or, in the case of drilled solid wood blocks, sanitized in an oven.

Some experts recommend using several small nests rather than one large one because large concentrations of bees may attract bee-eating birds and raccoons or cause a build-up of parasites. Having nests in several places also improves pollination efficiency because individual orchard mason bees rarely fly beyond 300 ft (92 m) from their nest.

Chapter 13

Carpenter Bees

Biology

Carpenter bees (*Xylocopa* spp., family Apidae) are large solitary bees that superficially resemble bumble bees in size and coloration. However, unlike bumble bees their abdomens are shiny, not hairy (Fig. 13.1). Males and females emerge in early spring and begin a frenzied mating season. The territorial males actively chase females and fight off other males, and this intense flight activity can be alarming to human bystanders. In spite of this, carpenter bees are only mildly defensive towards humans and the risk of stings is small. Females begin nesting and provisioning cells after they are mated. A female will excavate a long and branching tunnel in solid wood using her hardened mandibles. She prefers to occupy and enlarge an existing tunnel, but she may have to start a new one if old ones are not available. The female then forages for pollen and nectar, makes a pollen lump at the end of the tunnel, and lays an egg on it. She then repeats the process until she makes a succession of about ten cells back to back in the tunnel. She separates each cell with a partition of macerated wood which she scrapes from the wall of the tunnel (Fig. 13.2). Competition for nesting sites can be keen, and interloping females may take over a nest and eject the young while their mother is out foraging. In successful nests, the young emerge in summer and stay in the nest over autumn and winter. In Georgia, USA, females live at least 2 years, mating in their first year and nesting in their second (Gerling and Hermann, 1978). Exposed structural timbers are likely nesting sites, especially shaded rafters in a shed or under a porch. Carpenter bees can weaken structural wood after many years of activity.

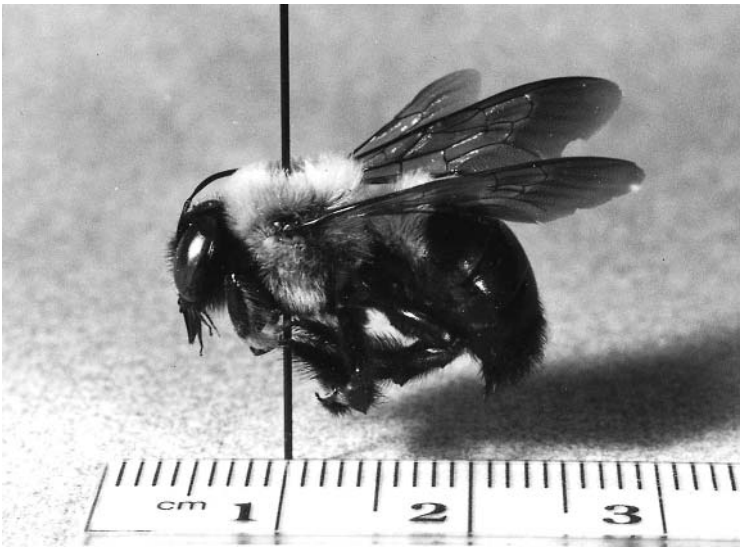


Fig. 13.1. A carpenter bee, *Xylocopa virginica*. The metallic-looking abdomen distinguishes it from the bumble bees whose abdomens are hairy. (Source: Nancy B. Evelyn.)

Carpenter Bees as Pollinators

The value of carpenter bees as crop pollinators is marginal in North America. They are effective pollinators of passion fruit (McGregor, 1976), and one species effectively pollinates cucurbits and sunflower in India (Sihag, 1993). In Georgia, USA, they visit blackberry, canola, maize, pepper, and pole bean (K.S. Delaplane, unpublished data), but their value on these crops is unknown. Carpenter bees may be useful as pollinators of buzz-pollinated crops such as tomato since they are capable of buzz-pollinating (Adams and Senft, 1994).

One of the best documented cases of carpenter bee pollination is in production of hybrid cotton in the southwestern US. When caged with male-sterile A-line cotton to exclude other pollinators, seven carpenter bees (*X. varipuncta*) provided as much seed cotton (seed + lint) as did one honey bee colony (Waller *et al.*, 1985b).

Carpenter bees are notorious for robbing flowers without contacting the anthers or stigma by cutting slits in the side of the flower in order to reach the nectaries. Nectar robbery by carpenter bees can be a serious problem in blueberry because the robbery holes attract other bee species which would otherwise legitimately visit the flower. In this manner as few as one carpenter bee per 25 bushes, or 4% incidence of slitted flowers, can induce 80–90% of the honey bees

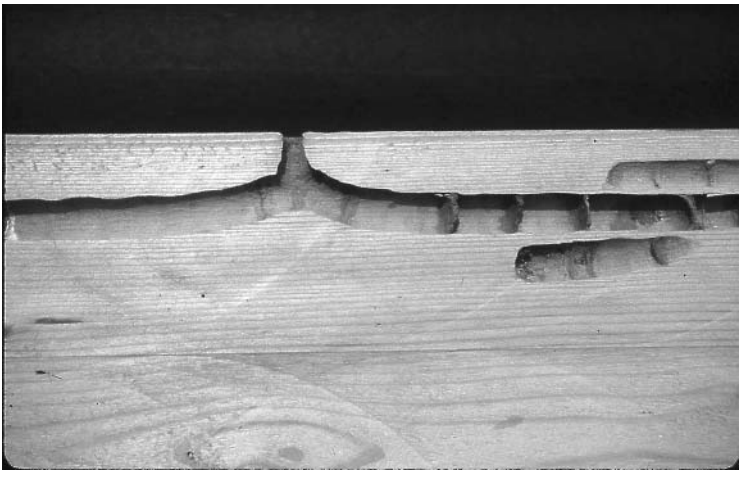


Fig. 13.2. A wooden board cut open to reveal a carpenter bee nest. The female separates each of about ten cells with a partition of macerated wood. The linear back-to-back pattern of the cells is typical of most tunnel-nesting solitary bees. (Source: Keith S. Delaplane.)

to switch to robbing (Cane and Payne, 1991). In south Georgia 100% of carpenter bees visiting rabbiteye blueberry were nectar robbers (Delaplane, 1995).

Chapter 14

Bees and Pesticides

Most bee poisonings occur when bees visit flowers that are treated with insecticide. This kind of exposure can be more hazardous than a spray landing directly on the outside of a bee hive or nest. Fast-acting toxins will quickly kill foraging bees in the field. However, it is the slower-acting toxins that are insidiously more hazardous because foraging bees survive long enough to return to the nest with contaminated pollen which then enters the food supply and kills brood over many weeks. Such affected colonies either die outright or become debilitated for the rest of the season.

Non-agricultural insecticides are also hazardous. In one study, honey bee colonies were experimentally exposed to ultra-low-volume sprays of malathion in order to simulate a mosquito control application (Pankiw and Jay, 1992). Compared to non-treated colonies, the sprayed colonies gained less weight, collected less pollen, had lower bee populations, and had lower numbers of bees foraging.

Sometimes insecticides do not kill bees but instead repel them from a crop and interfere with pollination. Honey bees were shown to be repelled from apple flowers sprayed with the insecticide dimethoate for at least two days after treatment (Danka *et al.*, 1985).

There is evidence that sub-lethal doses of insecticide can alter homing behaviour in foraging bees. In one study, a colony of honey bees was placed in an insect-proof cage and the workers trained to visit a feeder 8 m from the hive. Selected honey bees were then treated with sub-lethal doses of the insecticide deltamethrin and subsequently released. Of the treated bees, 81% failed to return to their nest within 30 s, a figure three times longer than the average time for non-treated bees (Vandame *et al.*, 1995). Considering the widespread use of insecticides in a typical agricultural landscape, it is possible that numerous similar sub-lethal effects are manifest and contributing to pollination problems.

It is a general principle that insecticides should never be applied to plants while they are flowering. However, there are occasions in which a crop must be treated for a serious pest even while the crop is in bloom. Fortunately, there are ways to reduce bee kill even in these situations.

First, it is important to underscore that not all insecticides are equally hazardous to bees, and bee species vary in their susceptibilities (Mayer *et al.*, 1994b). Appendix 3 rates some pesticides according to their relative hazard to bees based on the chemical's toxicity and its persistence after it is applied.

Secondly, the formulation of an insecticide affects its toxicity to bees. Granules and solutions are generally less hazardous than wettable powders and dusts. Non-sugary bait formulations are also relatively safe. For example, carbaryl-laced wheat bran flakes used to control rangeland grasshoppers are relatively safe to alfalfa leafcutting bees (Peach *et al.*, 1994, 1995).

Third, many insecticides are deadly to bees when they are first applied, but they degrade within hours to relatively non-hazardous levels. This means that certain acutely toxic insecticides can be applied in the late evening, and by morning the pest will be controlled and the residues will be sufficiently degraded so that day-flying bees can forage with relative safety (see Appendix 3). One exception to this scenario will be of concern to growers who rely on bumble bees or squash bees for pollination. These bees frequently spend the night in cucurbit flowers, and evening insecticide applications are no guarantee for their safety.

Finally, an emphasis on pest scouting, treatment thresholds, precision sprays, and other practices of *integrated pest management* (IPM) can be expected to reduce the number of sprays needed per season. IPM practices since the 1960s and 1970s in the western US have reduced the number of lucerne sprays per season from 6–8 to 1–3 with a noticeable benefit to pollinators (Peterson *et al.*, 1992).

Insecticidal bee kills are sometimes unacceptably high even in crops that bees rarely visit. This has been the case for bee-keepers in the southwestern US who report large bee kills following insecticide applications to blooming Bermuda grass grown for seed. In this case, bees apparently are exposed to the insecticide when they are forced to forage on Bermuda grass for lack of better forages (Erickson and Atmowidjojo, 1997). Moving bee colonies away from the area seems to be the only practical solution to a problem like this. In other cases, the bee exposure results when bees visit blooming weeds that are within the drift zone of a spray applied to a crop; Erickson *et al.* (1994) suggest clean cultivating to reduce this problem in snap bean.

Research in biological and botanical insecticides is yielding products that are safer for bees. Appendix 3 lists some of these

products, usually ones with the active ingredients *Bacillus thuringiensis* and diflubenzuron. Many of these products are specific to particular pest species and are relatively innocuous to non-target organisms. However, not all *B. thuringiensis* insecticides are safe for bees. For example, the label for XenTari® (Abbott Laboratories), with active ingredient *B. thuringiensis aizawai*, reads 'This product is highly toxic to honey bees exposed to direct treatment. Do not apply this product while bees are actively visiting the treatment area.'

Nevertheless, many biological insecticides are relatively safe for honey bees and may, in some cases, allow growers to spray crops during bloom, something inadvisable with 'harder' chemicals. For example, treating blooming canola with azadirachtin (an extract of the neem tree) at concentrations of up to 150 p.p.m. did not repel honey bees or other pollinators, and no residues of azadirachtin were found on the bodies of bees foraging on treated plants (Naumann *et al.*, 1994a). Certain doses of the insecticidal fungus *Metarhizium flavoviride* control pest locusts but kill relatively few honey bees (Ball *et al.*, 1994). These kinds of pesticides may be promising alternatives when growers are faced with emergency pest outbreaks during crop bloom.

One should always avoid untested mixes of two or more pesticides because the combined activity can be unpredictable. Sometimes a blend of two or more pesticides can be more toxic than any one of the ingredients by itself. This interactivity is called *synergism*. As an example, the insecticide Karate® is already highly toxic to honey bees (see Appendix 3), but when blended with the fungicides Impact® or Sportak® its toxicity increases up to 16 times (Pilling and Jepson, 1993).

Herbicides, plant growth regulators, and fungicides are relatively safe for bees but there are exceptions such as the herbicides 2,4-D and MSMA, the growth regulator carbaryl, and the fungicide binapacryl (Johansen and Mayer, 1990; Drexel Chemical Co., personal communication). Appendix 3 has bee toxicity information on certain herbicides and fungicides.

Sometimes insecticide-damaged honey bee colonies can be rehabilitated. The first step is to move hives away from the hazard. The colony may recover on its own if only the older adult population was affected and if it has plenty of honey and pollen. However, if brood and nurse bees continue dying then this means that the pollen is contaminated. In this case all combs with pollen must be removed. It may be possible to salvage these combs by soaking them in water for several hours, washing the pollen out of the cells, and air-drying, but it is safer simply to discard them. Weakened colonies can be fed to stimulate brood production. They can be strengthened with the addition of queenless packages of bees or combined together to make

up stronger colonies. It is important to quickly ascertain if the queen is still functioning normally and replace her if there are signs of reduced egg-laying capacity.

Obviously, pesticide applications must be clearly worked out between the grower and the bee-keeper. It is simple common sense to protect oneself with a pollination contract. Most contracts require the grower to give the bee-keeper a 24- to 48-h notice of a pesticide application (see Appendix 2).

Choosing the correct pesticide for any pest situation is a weighty matter. First, a pesticide should be used only if it is approved by governing authorities for the particular pest and site in question. Secondly, it is important to consider the best ways to protect groundwater and to conserve beneficial species such as pollinators and pest predators. Thirdly, there are sometimes other pest control practices available that can reduce or eliminate the need for pesticides. It is a blessing of the developed world that there is an abundance of information resources available to help farmers produce food and fibre in an environmentally responsible manner. Agricultural universities, extension services, crop consultants, and government departments of agriculture are good sources of research-based, environmentally sound pest control recommendations.

Chapter 15

Alfalfa (Lucerne) Seed

Flowering

Lucerne, also known as alfalfa (*Medicago sativa*), flowers occur on 1–4 in (2.5–10.2 cm) long racemes. The bottom flowers open first, and it takes about 7 days for flowering to proceed to the tip. Individual lucerne flowers are made up of a standard petal, two wing petals, and two keel petals joined at the base to form a corolla. The corolla encloses an ovary with 10–12 ovules, and a sexual column with a stigma and ten anthers (Fig. 15.1). The sexual column is held under tension within the two keel petals. When the flower is tripped, the sexual column snaps forward against the standard petal, releasing pollen. Tripping can occur spontaneously, but the tripping that causes cross-pollination occurs when a bee lands on the flower. The bee's probing activity releases the sexual column which snaps out of its enclosure and strikes the bee on its head. On the bee's head the stigma contacts pollen from other lucerne flowers. Flowers that are tripped may set seed; those that are not tripped do not set seed and instead wither and die. Once a flower is tripped the pollination process is finished.

Lucerne Pollination Requirements

The lucerne flower must be tripped in order to produce seed. For cross-pollination to occur the stigma must contact pollen from another lucerne plant. Although lucerne plants range from completely self-sterile to completely self-fertile, only 17–46% of self-pollinated flowers form seed pods (Free, 1993). Cross-pollination increases the rate of pollen tube growth, percentage of flowers forming seed pods, the number of seeds per pod, and the size of seeds. Compared to cross-pollinated seed, progeny of selfed plants are less productive in

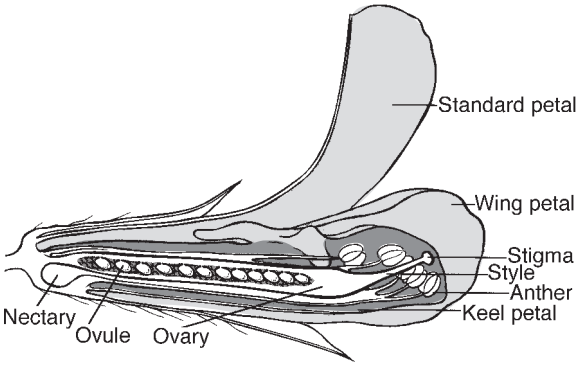


Fig. 15.1. Flower of lucerne, *Medicago sativa.* (Source: Darrell Rainey.)

either forage or seed production (McGregor, 1976). Fortunately, the amount of natural cross-pollination in lucerne fields is around 90% (Free, 1993).

Environmental factors (dryness) can cause some spontaneous tripping in flowers (around 5% in North America) without insect visits. However, this results in self-pollination and is not conducive to optimal seed yields.

Lucerne Pollinators

Lucerne must be cross-pollinated in order to produce large amounts of good quality seed, and flower tripping by bees is the only practical method of cross-pollinating lucerne. Tripping is irreversible because the stigma lodges in the groove of the standard petal. Cross-pollination occurs when a bee carrying pollen from previous flowers trips the flower. Subsequent bee visitors to the same flower no longer cause cross-pollination.

Honey bees as lucerne pollinators

Honey bees are the primary lucerne pollinator in California, Arizona, and to some extent southern Nevada. Pollen-collecting honey bees that trip flowers make up 20–100% of the pollinator force in these areas. Nectar collectors contribute a little to lucerne pollination by accidently tripping the flowers; this happens with about 2% of the flowers. Lucerne seed yields resulting from honey bee pollination in the south-

western US are as high as 1000 lb acre^{-1} (1120 kg ha^{-1}) (Robinson *et al.*, 1989).

In the northern US and Canada, pollen-collecting honey bees average only 0–1% of the pollinator force, and nectar collectors accidently trip about 0.2–0.3% of the flowers. Honey bees are more effective in certain isolated valleys of northern Nevada, even at high elevations, where there is less competition from other pollen plants.

Honey bees are not acceptable lucerne pollinators in all areas. They are not recommended in Canada (Reinhardt, 1953) nor in Washington (Johansen, 1974). Their colonies placed near lucerne may repel other bee visitors (Pesenko and Radchenko, 1993).

Colonies used to pollinate lucerne should be strong with a laying queen and eight or more frames covered with bees in a two-storey hive. Colonies must have plenty of brood, especially young brood that stimulates workers to forage for pollen. Colonies are often placed in fields in two waves – the first colonies go in when the lucerne is about one-third in bloom, and the second wave goes in at or just past one-half bloom. Most seed is set within a 300-ft (92 m) radius of a colony. Colonies should be deposited in groups of 12–18 per location with about 480 ft (146 m) between locations.

Honey bees visit lucerne most readily when flowering plants are slightly moisture stressed rather than when the plants are freshly irrigated or too dry. If entire blocks are irrigated on the same schedule, at any one time the entire block may be unattractive to honey bees, that is, either too wet or too dry, and bees will learn to visit competing bloom. This problem can be minimized by irrigating sections of a block in an alternate fashion so that bees always have access to attractive lucerne.

Watering barrels should be placed near hives to keep bees from visiting distant sources of water; if bees must travel far to get water, fewer of them are free to pollinate the crop. Two big barrels of water for each 45 acres (18.2 ha) is recommended, and they must be refilled as needed. Water barrels should have some kind of float on the surface to keep bees from drowning.

Honey bees often learn to avoid visiting lucerne, apparently in response to the experience of receiving a blow to the head when the flower is tripped. Such learned avoidance does not occur with alkali bees or leafcutting bees. However, honey bees respond well to breeding programmes aimed at overcoming this liability. Nye and Mackenson (1968, 1970) selected a strain of honey bee that preferentially collected lucerne pollen; however, the programme was abandoned. In later work, three generations of selection yielded a 'high pollen-hoarding strain' of honey bee that when placed near lucerne stored 2.4 times more pollen than did a 'low-strain' (Gordon *et al.*, 1995). Although the 'high-strain' did not prefer lucerne pollen, its

overall higher pollen collection rate probably enhanced lucerne pollination because pollen-collecting bees are generally better pollinators. Unfortunately, today there are no commercially-available stocks of honey bee selected for high pollen-hoarding behaviour.

Alkali bees as lucerne pollinators

Alkali bees (Chapter 9) are widely used in the Touchet area of Washington and in Nevada. A 1 acre (0.4 ha) alkali bee bed with an average of 1 million nesting females (2.5 million ha^{-1}), provides excellent pollination for 200 acres (81 ha) of lucerne grown for seed. Although these native bees are excellent pollinators of commercial lucerne in western North America, in recent years they have been largely supplanted by alfalfa leafcutting bees.

Leafcutting bees as lucerne pollinators

Alfalfa leafcutting bees (Chapter 11) are the most important lucerne pollinators in the northwestern US, Canada, and to some extent California. Each female can pollinate enough lucerne blossoms to set $\frac{1}{4}$ lb (0.1 kg) of seed. Most growers aim for 20,000 bees (7000 female bees) $acre^{-1}$ or 50,000 bees (18,000 females) ha^{-1}. Seven thousand females per acre can set a field in 10–14 days under ideal conditions. Bees are sold while they are dormant in cells, either by the gallon or in wooden nest boards. In spite of its name, the alfalfa leafcutting bee is often highly attracted to other crop plants, including white sweet clover and purple loosestrife (Small *et al.*, 1997).

Non-managed bees as lucerne pollinators

Lucerne is attractive to a large number of bee species, many of which doubtless provide valuable pollination services. In 20 lucerne plantations in Canada (16 near Ottawa, Ontario; 4 in the Peace River region), the largest number of bee visitors were leafcutting bees (*Megachile* spp.), followed by bumble bees. Honey bees were the fifth-most frequent lucerne visitors, and no alkali bees were found (Brookes *et al.*, 1994). The researchers avoided sampling managed leafcutting bees (*M. rotundata*) by sampling bees no nearer than ~300 ft (90 m) from artificial bee shelters; managed honey bees were never nearer than 1.2 miles (2 km) at every sampling site. Lucerne was not the most attractive bee plant in the sampled areas; there were three other plant species more heavily visited. However, lucerne seemed to benefit from

Table 15.1. Recommended bee densities for lucerne.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
3–6 (7.4–14.8)	Todd and Vansell (1952)
2–4 (4.9–9.9)	Vansell and Todd (1946); Hobbs and Lilly (1955); Bohart (1957); McGregor (1976, 1981); Crane and Walker (1984); Levin (1986); Berg (1991)
1–3.2 (2.5–8)	Williams (1994)
3.2 (7.9)	**Literature average**
Other measures and bees	
2–7 honey bee nectar foragers yd^{-2} (2.4–8.4 m^{-2})	Jones (1958)
3000 alkali bees acre^{-1} (7410 ha^{-1})	Mayer and Lunden (1993)
1 leafcutting bee 5 yd^{-2} (1.2 5 m^{-2})	Bohart (1967)
20,000–50,000 leafcutting bees acre^{-1} (50,000–123,500 ha^{-1})	Strickler *et al.* (1996)
20,000 leafcutting bee cells acre^{-1} (50,000 ha^{-1})	Kevan (1988)
6000–16,000 leafcutting bee cells acre^{-1} (15,000–40,000 ha^{-1})	Scott-Dupree *et al.* (1995)

the presence of other blooming plants that attracted pollinators. Bee visitation was much heavier in lucerne growing within 33 ft (10 m) of blooming wildflowers than it was in the middle of large lucerne fields. Seed yield at one site pollinated only by wild bees was 214 lb acre^{-1} (240 kg ha^{-1}) which is within the range expected for non-irrigated fields.

Chapter 16

Almond

Flowering

The almond (*Prunus dulcis*) flower has one pistil with one ovary containing two ovules, 10–30 stamens, and five pinkish-white petals. Usually only one ovule develops into a fruit. Nectar is excreted into a floral cup at the base of the pistil (Fig. 16.1). The plant blooms from late January to late March, and bees readily visit the flowers for pollen and nectar. Spain is the principal almond producer in Europe. In the US, practically all commercial almond is grown in California.

Almond Pollination Requirements

Almond is completely self-incompatible and must be cross-pollinated with pollen from a different plant and variety. The pollination requirements of almond are extraordinarily high. While most other orchard crops need 5–10% fruit-set to make a viable crop, almond requires 30–60% (Traynor, 1993). Not all pollinated flowers set fruit, and unlike apple and other orchard crops, almond is not thinned. This means that virtually 100% of the flowers must be cross-pollinated to achieve an acceptable crop.

'Nonpareil' is the most important almond cultivar in California. 'Nonpareil' is interplanted in alternating rows with compatible pollenizer varieties such as 'Carmel', 'Fritz', 'Merced', 'Monterey', 'Price', or 'Sonora'. A 1:1 or 1:1:1 interplant scheme is preferred; that is, one row of 'Nonpareil' grown next to one or two rows of pollenizer varieties. Experience from the 1940s and 1950s showed that higher ratios of main variety to pollenizer – 4:1 or 2:1 – cause lower yields in those main variety rows that are furthest from the pollenizer (Traynor, 1993). It is important that all interplanted varieties are cross-compatible; there

Table 16.1. Cross-incompatible groups (CIGs) for California almond varieties (Kester *et al.*, 1994). Varieties within the same CIG group should not be grown together.

Group	Varieties
CIG-I	Nonpareil, I.X.L., Long I.X.L., Profuse, Tardy Nonpareil
CIG-II	Mission, Ballico, Languedoc
CIG-III	Thompson, Robson, Harvey, Granada, Sauret #2, Mono, Wood Colony
CIG-IV	Merced, Ne Plus Ultra, Price Cluster, Norman, Ripon, Rosetta
CIG-V	Carmel, Carrion, Sauret #1, Livingston, Monarch
CIG-VI	Monterey, Seedling 1–98
CIG-VII	Sonora, Vesta, Solano, Kapareil

are at least seven reciprocally cross-incompatible variety groupings used in California (Table 16.1).

'Jeffries' is a high-yielding mutation of 'Nonpareil', but it is unilaterally incompatible. In this case, this means that all varieties can fertilize 'Jeffries', but 'Jeffries' cannot fertilize 'Nonpareil', all CIG-V, CIG-VI, and CIG-VII groups, or 'Butte', 'Grace', and 'Valenta' (Traynor, 1993; Kester *et al.*, 1994).

In planning an orchard, it is necessary to select compatible varieties whose bloom periods overlap. Varieties should be chosen so that they bloom within three days of each other. If possible, it is preferable to select pollenizers that bloom shortly before the main variety rather than after. Table 16.2 is a helpful guide for selecting varieties for good bloom overlap. Varieties also differ in frost-hardiness and in quantities of pollen produced. Agricultural extension services and crop consultants can help one select varieties for a particular location.

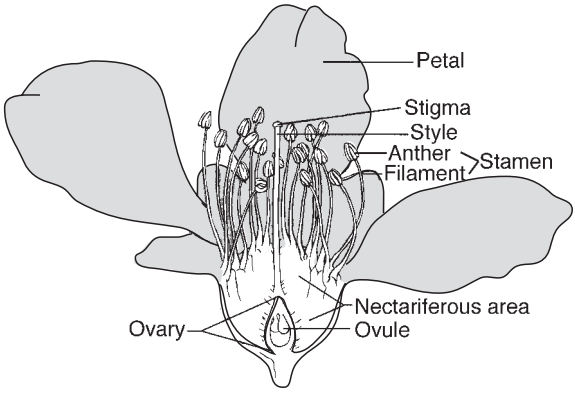


Fig. 16.1. Flower of almond, *Prunus dulcis*. (Source: Darrell Rainey.)

Table 16.2. Bloom period of almond varieties relative to 'Nonpareil'. Numbers indicate days before (−) or after (+) average peak 'Nonpareil' bloom (Traynor, 1993).

Early	Early-mid	Mid	Late-mid	Late	Very late
Ne Plus (−6)	Sonora (−3.5)	Nonpareil (0)	LeGrand (+3)	Butte (+5)	Ripon (+12)
	Peerless (−2.5)	Jeffries (0)	Tokyo (+3)	Padre (+5)	Planada (+14)
	Milow (−1)	Price (0)	Drake (+3)	Thompson (+5)	Tardy Nonpareil (+17)
		Kapareil (+1)	Monarch (+3)	Livingston (+5)	
		Suaret #1 (+1)	Suaret #2 (+3)	Mission (+5)	
		Carmel (+2)	Norman (+4)	Mono (+7)	
		Monterey (+2)		Yosemite (+7)	
		Carrion (+2)		Ruby (+8)	
		Fritz (+2.5)			
		Merced (+2.5)			
		Harvey (+2.5)			
		Solano (+2.5)			

If possible, it is a good idea to plant blocks of mid- and late-blooming varieties next to each other (with the usual 1:1 or 1:1:1 interplant of compatible varieties within each block). By placing bee hives between blocks, one can conceivably get twice as much work out of the rented hives; bees will pollinate the mid-blooming block one week and the late block the next.

Almond Pollinators

Honey bees as almond pollinators

Honey bees are the most important pollinator of almond in the US (Table 16.3). They readily visit almond flowers and effectively pollinate them. Because almond's pollination demands are so high, it is doubly important to use strong colonies. The goal is to have colonies at peak strength at the time of peak bloom. An acceptable colony will have eight frames of bees – a 'frame' meaning one standard deep frame two-thirds to three-quarters covered with bees at 60°F (15.6°C) (Traynor, 1993) – and 800 in^2 (5200 cm^2) of brood (McGregor, 1976). However, because the bloom season for almond is so early in the year it is sometimes difficult for bee-keepers to have colonies at full strength. Bee-keepers can stimulate colony growth with a mid-winter feeding programme, but this is costly and many choose instead to rent weaker colonies at a reduced fee. Most almond pollination contracts are based on an average number of frames of bees; a grower that wants a minimum frame standard must be willing to pay a higher fee because every colony must be inspected. County agriculture commis-

sioner offices, private consultants, and some brokers offer colony strength inspection services.

A second problem posed by early-blooming almond is cool weather. Honey bees do not fly readily until temperatures exceed 55°F (12.8°C). One way to minimize this problem is to put hives in sunny, wind-protected locations to encourage good flight. If cool temperatures persist, it may be necessary to increase hive density in order to compensate for reduced flight efficiency.

With many other crops it is advisable to bring in bees after some bloom has already begun. This is not the case with almond because the earliest blooms are the most productive. Moreover, there is usually little else blooming to distract the bees, and honey bees eagerly visit almond as soon as it starts blooming. So, there is no reason to delay the arrival of bees and most growers bring in bees as soon as the crop blooms, or earlier. If early-blooming apricots, mustard, or peaches are present to compete with almond, a bee attractant may help (see Chapter 7, page 58). However, there is no evidence that bee attractants are effective on almond (M.L. Winston, Simon Fraser Univ., personal communication).

McGregor (1976) recommends placing colonies within an orchard in groups spaced $\frac{1}{10}$ mile (160 m) apart. But it seems that having strong colonies is more important than their distribution in the orchard. Growers achieve good results when large groups of strong colonies are placed along roadways $\frac{1}{4}$–$\frac{1}{2}$ mile (0.4–0.8 km) apart within the orchard (Traynor, 1993). As with other crops, bee hives placed together in large groups perform better than hives distributed singly. Hives in California are usually deposited in groups of 16, 24, or 32.

Webster *et al.* (1985) showed in almond orchards that honey bee hives fitted with pollen traps fielded a higher proportion of foragers collecting pollen compared to non-modified hives. This potential benefit, however, was partially offset by a slower rate of growth in those colonies with traps.

Table 16.3. Recommended bee densities for almond.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
2–3 (5–7)	McGregor (1976)
1–3 (2.5–7)	Thorp and Mussen (1979)
3–4 (7–10)	Levin (1986)
2 (5)	Traynor (1993); Scott-Dupree *et al.* (1995)
2.5 (6)	**Literature average**
Other bees	
3 *O. cornuta* females per tree (in Spain)	Bosch (1994b)

Orchard mason bees as almond pollinators

Two orchard mason bees are potential pollinators of almond – the North American native blue orchard bee (*O. lignaria propinqua*) and the orange orchard bee (*O. cornuta*) from Spain (Chapter 12). When introduced into California almond orchards, both bees collect almond pollen, occupy man-made nests, and develop normally on a diet of almond pollen and nectar (Torchio, 1981a,b; Torchio *et al.*, 1987). However, many females disperse away from February release sites before nesting. These bees are good pollinators; in Spain, each *O. cornuta* female visits 9500–23,600 almond flowers during a season, and only three females per tree are needed to maximize pollination (Bosch, 1994b). However, the technology for their large-scale, practical use is not yet developed.

Chapter 17

Apple

Flowering

The apple (*Malus domestica*) flower occurs in a cluster of flowers at the end of a 1–3-year-old woody shoot called a *spur*. The flower has five stigmas that join into a style that leads to the ovary (Fig. 17.1). The ovary has five divisions, each with two ovules, which means that a fully-pollinated fruit will have ten seeds (the variety 'Northern Spy' has four ovules per division for a maximum of 20 seeds). Surrounding the style are 20–25 pollen-bearing stamens. Nectar is excreted at the base of the central style. Five pinkish-white petals surround the sexual parts. Each flower cluster has a primary bud called the *king bloom* that opens first and produces the best fruit. Production of nectar and pollen is marginal to good, and bees readily visit the blossoms.

Apple Pollination Requirements

At least 6–7 ovules must be fertilized. If this threshold is not met then the fruit will be misshapen (Brault and de Oliveira, 1995), small, or may not stay on the tree until harvest (McGregor, 1976). Inadequate pollination can also reduce calcium concentrations in fruit (Volz *et al.*, 1996) which can predispose the fruit to storage problems (Ferguson and Watkins, 1989).

Most apple varieties require cross-pollination with another compatible variety. Some exceptions to this are the varieties 'Newtown' and, to a lesser extent, 'Golden Delicious' and 'Rome Beauty'. Many varieties show a degree of self-fruitfulness, but not enough to allow solid-block plantings. So orchardists must interplant main varieties with compatible pollenizer varieties. Generally, closely-related varieties – as, for example, McIntosh, Early McIntosh, Cortland, and

Fig. 17.1. Flower of apple, *Malus domestica*. The flower has been partially dissected to reveal interior structures. (Source: (art) Darrell Rainey; (photo) Jim Strawser.)

Macoun – do not cross-pollinate each other well. Likewise, spur types do not pollinate the parent variety well. The bloom periods of the main and pollenizer varieties must overlap. To optimize pollination, it is necessary to plant both early- and late-blooming pollenizers so that the main variety blooms in between. In that way, ample pollen will be available for the early-blooming king bloom on the main variety, and if frost kills the king blooms the late-blooming pollenizers will provide pollen for those flowers that remain.

Some apple varieties have sterile pollen. These varieties willingly receive pollen from other varieties and produce fruit, but they cannot

Table 17.1. Apple varieties, pollen viability, and relative bloom periods for the southeastern US (from Horton *et al.*, 1990).

Variety	Good pollenizer interplants	Pollen viability	Relative bloom period (days)								
Winter Banana (Spur)	✓	Good	X	X	X	X	X	X	X		
Jersey Mac	✓	Good	X	X	X	X	X	X			
Empire		Good	X	X	X	X					
Paulared		Good		X	X	X	X				
Stayman		Not good		X	X	X	X				
Yates	✓	Good		X	X	X	X	X			
Jonagold		Not good			X	X	X	X			
Delicious		Good			X	X	X	X			
Braeburn		Good			X	X	X	X			
Mutsu		Not good			X	X	X	X			
Jonathan		Good				X	X	X	X		
Granny Smith		Good				X	X	X	X	X	
Arkansas Black		Good				X	X	X	X		
Gala		Good				X	X	X	X		
Golden Delicious		Good				X	X	X	X		
Fuji		Good				X	X	X	X	X	
Rome Beauty		Good					X	X	X	X	X

Table 17.2. Apple and crabapple varieties and relative bloom periods for interior British Columbia (British Columbia Ministry of Agriculture, Fisheries and Food, 1994).

Variety	Relative bloom period (days)														
Dolgo	X	X	X	X	X	X	X								
Sunrise	X	X	X	X	X	X	X	X	X	X					
Makamik		X	X	X	X	X	X	X							
Empire		X	X	X	X	X	X	X	X						
McIntosh			X	X	X	X	X	X	X						
Golden Delicious				X	X	X	X	X	X	X					
Jonagold				X	X	X	X	X	X	X	X				
Elstar				X	X	X	X	X	X	X	X	X			
Manchurian					X	X	X	X	X	X	X	X			
Spartan						X	X	X	X	X	X	X	X		
Red Delicious						X	X	X	X	X	X	X	X		
Royal Gala							X	X	X	X	X	X	X	X	
Rome Beauty							X	X	X	X	X	X	X	X	
Fuji							X	X	X	X	X	X	X	X	
Winter Banana							X	X	X	X	X	X	X	X	
Granny Smith							X	X	X	X	X	X	X	X	
Braeburn									X	X	X	X	X	X	X

Table 17.3. Apple varieties and suitable pollenizers for interior British Columbia (British Columbia Ministry of Agriculture, Fisheries, and Food, 1994).

Main variety	Pollenizer
McIntosh	Crabapples Dolgo and Garry, Discovery, or other early-blooming variety
Spartan	Red Delicious, Golden Delicious, Winter Banana
Golden Delicious	Spartan or Red Delicious
Red Delicious	Spartan, Golden Delicious, Spur Winter Banana
Empire	McIntosh
Jonagold	McIntosh, Empire, Spartan
Gala, Braeburn, Fuji	These can pollinate each other. Red Delicious, Granny Smith, and Winter Banana are also suitable pollenizers

be used as pollenizers. Tables 17.1–17.4 list some apple varieties, their pollen viabilities, and relative bloom intervals for various regions of North America. Nursery stock catalogues also list main varieties and compatible pollenizers.

Insects are the only practical pollinators of apple. A mechanical power pollen duster device was shown to have no effect on fruit set, fruit size, seed number, or yield (Schupp *et al.*, 1997).

Growers can use flowering crabapples as pollenizers instead of another commercial variety. This is warranted if other candidate pollenizers produce inferior fruit, take up too much orchard space, have conflicting pesticide requirements, or produce fruit that pickers cannot distinguish from the main variety. The flower colour of a crab variety should match the colour of the main variety since bees do not readily switch to a different-coloured blossom during a foraging trip (Mayer *et al.*, 1989b). Crabapples can be planted in existing space between main variety trees or grafted on to them; this makes crabapples an attractive remedy for old orchards that were not interplanted with pollenizers.

One can cut bouquets of flowering crabapples (or of any pollenizer) and place them in barrels of water between rows during bloom. Such bouquets should be cut only when the king bloom is open, and they should be made large. It is helpful to change water when blooms begin to wilt and to place bouquets in sunny, still areas.

Because crabapples bloom on 1-year-old wood, crabapples should be pruned immediately after bloom in order to get them ready for next year. Some crabapples are more susceptible to virus diseases, but whole-tree crabapple plantings, rather than grafts, can reduce this problem. If crabs are grafted into virus-infected main variety trees, the grafts may fail because of virus-induced graft incompatibility.

Bees prefer to work up and down rows rather than across rows. This is especially true in dense plantings and during even the lightest wind. One must consider this when planning the arrangement of main

Table 17.4. Apple varieties, compatibilities, and season of bloom for the northwestern US. Blank boxes indicate suitable pollenizer combinations. A '0' indicates varieties that are not suitable pollenizers for each other. An 'X' indicates that the variety is partially self-fruitful but should not be planted in solid blocks.

Pollen source variety		Variety pollinated: Early bloom								Midseason bloom																	Late bloom			
		Lodi	Earligold	Jonamac	Gravenstein	McIntosh	Spartan	Liberty	Idared	Scarlett Gala	Akane (Prime Red)	Jonathan	Stayman	Jonagold	Mutsu (Crispin)	Cotland	Empire	Enterprise	Golden Delicious	Red Delicious	Spur Winter Banana	Winesap	Newton Pippin	Granny Smith	Fuji	Braeburn	Ramey York	Rome	Northern Spy	Lady
Lodi	Early bloom	X																									0	0	0	0
Earligold	Early bloom		X																								0	0	0	0
Jonamac	Early bloom			0																							0	0	0	0
Gravenstein	Early bloom	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
McIntosh	Early bloom			0		0																					0	0	0	0
Spartan	Early bloom						X																				0	0	0	0
Liberty	Early bloom							X																			0	0	0	0
Idared	Early bloom								X																		0	0	0	0
Scarlett Gala	Midseason bloom									X																				
Akane (Prime Red)	Midseason bloom										X																			
Jonathan	Midseason bloom											X																		
Stayman	Midseason bloom	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jonagold	Midseason bloom	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mutsu (Crispin)	Midseason bloom	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotland	Midseason bloom															X														
Empire	Midseason bloom																X													
Enterprise	Midseason bloom																	X												
Golden Delicious	Midseason bloom													0					X											
Red Delicious	Midseason bloom																			0										
Spur Winter Banana	Midseason bloom																				X									
Winesap	Midseason bloom	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Newton Pippin	Midseason bloom																						X							
Granny Smith	Midseason bloom																							X						
Fuji	Midseason bloom																								X					
Braeburn	Midseason bloom																									X				
Ramey York	Late bloom	0	0	0	0	0	0	0	0																		X			
Rome	Late bloom	0	0	0	0	0	0	0	0																			X		
Northern Spy	Late bloom	0	0	0	0	0	0	0	0																				X	
Lady	Late bloom	0	0	0	0	0	0	0	0																					X

Fig. 17.2. Plan 1 orchard design for encouraging apple cross-pollination. Every other tree is a pollenizer. (Source: Carol Ness.)

and pollenizer varieties in an orchard. With orchard plan 1, every other tree is a pollenizer (Fig. 17.2); this maximizes the number of pollenizers, but it is practical only if there is a market for the pollenizer. All other plans compromise some degree of pollination efficiency in favour of convenience at harvest. With plan 2, every third tree in every third row is a pollenizer (Fig. 17.3); this ensures that every tree of the main variety is next to, diagonal to, or across from a pollenizer on one side. Plan 3 calls for a solid planting of the pollenizer every fourth row (Fig. 17.4); this leaves one row of main variety by itself and is practical only if the pollenizer has market value. Plan 4 calls for two pollenizer rows next to four rows of the main variety (Fig. 17.5); this is the least efficient design. Main varieties and their pollenizers should not be planted in the same row, as in plans 1 and 2, if they cannot withstand the same chemical regimen. Instead, pollenizers should be planted in their own rows so that they can be treated separately, as in plans 3 and 4. Crabapple pollenizers can be pruned for tall growth to take up little or no extra space. In this manner, they can be planted as every sixth to ninth tree in every row.

Apple Pollinators

Honey bee efficiency

Honey bees are the most important pollinator of apple in North America (Table 17.5). Honey bees usually work apple blossoms readily, but apple is not always the richest available forage and competing bloom can be a problem. Although honey bees pollinate apple well, they are not the most efficient apple pollinator. They sometimes rob an apple flower of its nectar without pollinating it; this happens most often with the 'Delicious' apple variety. Honey bees make fewer contacts with the sexual column of the apple flower, compared to certain solitary bees.

Researchers have increased apple visitation by honey bees with pheromone-based bee attractants (R.D. Fell, unpublished report; Mayer *et al.*, 1989a; Currie *et al.*, 1992b). Thus, emerging technology and honey bees' naturally large foraging populations may serve to partly compensate for their relative inefficiencies in apple.

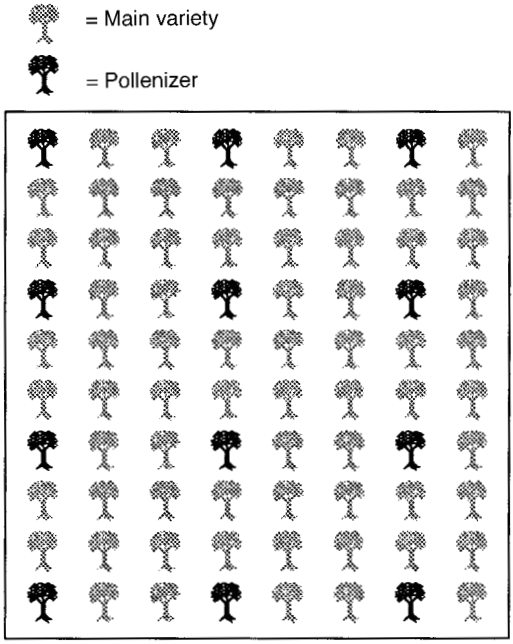


Fig. 17.3. Plan 2 orchard design for encouraging apple cross-pollination. Every third tree in every third row is a pollenizer. (Source: Carol Ness.)

Honey bee colony strength standards

As with any early-blooming crop, it can be difficult to get strong colonies in time for apple bloom. As much as possible, colonies should have large adult populations and plenty of brood (see Chapter 7, page 51). Mayer *et al.* (1986) and Ambrose (1990) recommend a minimum strength standard of six frames of brood covered by adult bees. Such a colony will have about 20,000 bees.

Managing honey bee hives for apple pollination

In smaller orchards, colonies should be placed in groups of 4–6 at 150-yard (137 m) intervals. With larger orchards, colonies should be placed in groups of 8–16 at 200–300-yard (183–275 m) intervals, starting about 100 yards (92 m) from the edges. Young trees, with fewer blossoms, are less attractive to bees than older trees, so in young orchards the grower may have to increase hive numbers in order to compensate (Mayer *et al.*, 1986).

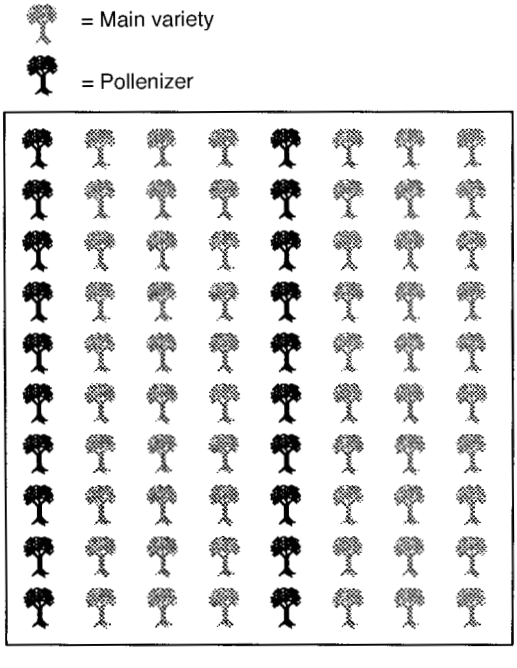


Fig. 17.4. Plan 3 calls for a solid planting of the pollenizer every fourth row. (Source: Carol Ness.)

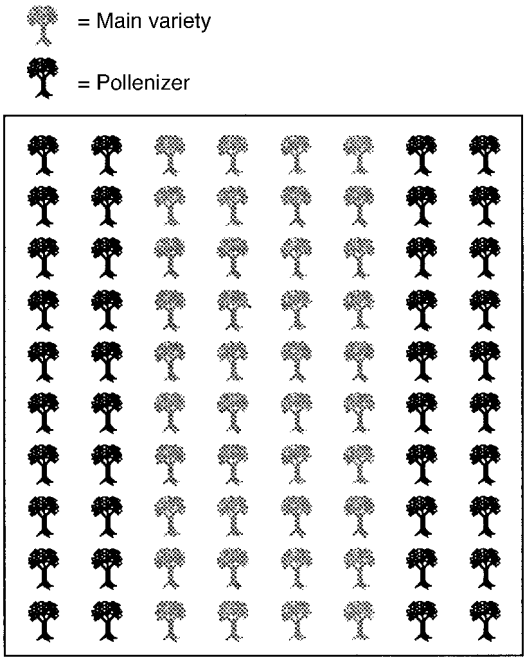


Fig. 17.5. Plan 4 has two pollenizer rows next to four rows of the main apple variety. (Source: Carol Ness.)

Colonies should not be kept at the apple orchards year-round. Instead, they should be moved in after about 5% of the orchard is in bloom or when the first king blooms open. Such a delay will encourage bees to focus on the crop rather than learn to visit competing plants.

Pollen dispensers (hive inserts) are devices that fit at the entrance of bee hives and hold pollen of desirable pollenizer varieties in such a way that bees dust themselves with the pollen as they leave the hive. Although dispensers have a questionable record (Jay, 1986; Mayer *et al.*, 1986), many apple growers use them. Like crabapples, pollen dispensers are an attractive remedy for old solid-block orchards with no pollenizers planted nearby (Anonymous, 1983; Mayer and Johansen, 1988). In general, inserts are warranted when weather restricts the blooming of pollenizers and the activity of the bees.

It is necessary to use only pure, hand-collected apple pollen in dispensers; cured, pollen-laden anthers are even better (Mayer *et al.*, 1986). Bee-collected pollen pellets will not pollinate apple flowers, even though they are easily obtained from pollen traps at hive entrances. *Lycopodium* powder is sometimes used to dilute pollen, but it agitates bees and is no longer recommended. High-quality

pollen for inserts is available commercially. Pollen should be kept refrigerated until use, and inserts should be replenished with about a teaspoon of pollen every few hours while bees are actively flying. A bee density rate of two bee hives per acre (5 ha^{-1}) is recommended if one is relying on inserts for pollination (Mayer *et al.*, 1986).

Orchard mason bees as apple pollinators

Orchard mason bees (*O. cornifrons, O. lignaria lignaria,* and *O. lignaria propinqua*) (Chapter 12) are potential apple pollinators. *O. lignaria lignaria,* and *O. lignaria propinqua* land directly on the anthers and stigma of the blossom, thus maximizing the chance of successful pollination (Torchio, 1985). Honey bees, on the other hand, sometimes land on the flower petals before approaching the sexual column. In a comparison of orchard bees and honey bees in Japan, orchard bees visited more apple flowers per minute and contacted the sexual column 26 times more frequently (Batra, 1982). Orchard bees are most promising in cases where honey bees are not available or in those varieties that honey bees work inefficiently, such as 'Delicious'. In North Carolina, *O. lignaria lignaria*,

Table 17.5. Recommended bee densities for apple.

No. of honey bee hives $acre^{-1}$ (ha^{-1})	Reference
1(2.5)	Humphry-Baker (1975); Crane and Walker (1984); Ambrose (1990); Kevan (1988)
2 (5)	Mayer *et al.* (1986)
0.25, 0.5, 1, 2 (0.6, 1.2, 2.5, 5)	McGregor (1976)
1–2 (2.5–5)	Levin (1986)
0.4–2 (1–5)	Kevan (1988)
0.8–1.2 (2–3)	British Columbia Ministry of Agriculture, Fisheries, and Food (1994)
1.5–5 (4–12.5)	Scott-Dupree *et al.* (1995)
1.5 (3.7)	**Literature average**
Other measures and bees	
20–25 honey bees per tree per observation min	Mayer *et al.* (1986)
75 honey bees leaving hive entrance min^{-1}	Ambrose (1990); Mayer *et al.* (1986)
1 honey bee per 1000 flowers	Palmer-Jones and Clinch (1968)
6 honey bee visits per flower	Petkov and Panov (1967)
250 orchard bees $acre^{-1}$ (618 ha^{-1})	Torchio (1985)
2834 orchard bees $acre^{-1}$ (7000 ha^{-1})	Batra (1982)

O. lignaria propinqua, and *O. cornifrons* improved fruit-set, seed number, and fruit shape in 'Delicious' apples, even in areas of orchards that already had honey bee hives (Kuhn and Ambrose, 1984). In spite of these favourable studies, orchard mason bee management has not reached practical large-scale levels. Recurring problems include the timing of bee emergence with apple bloom, the dispersal of females away from the orchard after release, and disease contamination in nest materials.

*Soil-nesting bees (non-*Nomia*) as apple pollinators*

Populations of non-managed soil nesters range from abundant to insignificant. Some soil nesters are good apple pollinators where they occur in large numbers. In Maryland, the introduced *A. pilipes villosula* is active during apple bloom. It forages in cool, damp weather, and works from before dawn to after dusk (Batra, 1994). Small-scale culturing methods are worked out (S.W.T. Batra, unpublished report).

Leafcutting bees as apple pollinators

Managed leafcutting bees (*M. rotundata*) will visit apple blossoms in Washington, but they fly only when temperatures are greater than 75°F (24°C) (D.F. Mayer, unpublished data). Moreover, the bees must be incubated starting 21 days before bloom, and it is not easy to predict apple bloom.

Chapter 18

Asparagus Seed

Flowering

The male (staminate) and female (pistillate) flowers of asparagus (*Asparagus officinalis*) usually develop on different plants, although some perfect flowers occur. Early-stage flowers are similar and have both male and female organs. One set of organs usually aborts, leaving the flower, and plant, either male or female. Male flowers (Fig. 18.1) are slightly larger than the females (Fig. 18.2) and open first. The flower has six major segments, six stamens (poorly developed in the pistillate flower), and a three-lobed pistil (poorly developed in the staminate flower). Both kinds of flowers have nectaries at the base of the corolla. The individual whitish-green flowers are pendulous, bell-shaped, and about $\frac{1}{4}$ in (0.6 cm) long. Flowers produce nectar and pollen and attract bees.

Asparagus Pollination Requirements

The flower design nearly assures cross-pollination. Pollen must be transferred from male flowers (plants) to female ones in order for seed to be produced. This must happen in the morning while pollen is available and before it dries out. Pollen is not carried by wind, so insect pollination is the rule. Growers should make sure that there is at least one male plant within 5 ft (1.5 m) of each female and one male for each six female plants (McGregor, 1976).

Table 18.1. Recommended bee densities for asparagus.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
1–2, 2 (2.5–5, 5)	McGregor (1976)
1.7 (4)	**Literature average**

Fig. 18.1. Male flower of asparagus, *Asparagus officinalis*. (Source: Darrell Rainey.)

Fig. 18.2. Female flower of asparagus, *Asparagus officinalis*. (Source: Darrell Rainey.)

Chapter 19

Avocado

Flowering

A mature avocado (*Persea americana*) tree may bear 1 million flowers in one season. Flowers occur on terminal panicles, and new flowers open daily during flowering season. Each flower is about $\frac{1}{2}$ in (1.3 cm) wide, $\frac{1}{2}$ in deep, and perfect, housing both male and female parts (Fig. 19.1). The single pistil has an ovary, an elongated style, and a stigma. Surrounding the pistil are nine stamens. Flowers produce nectar and pollen and attract bees. However, other plants, namely citrus and mustard, can bloom at the same time and compete with avocado for pollinators.

Each avocado flower opens twice in two consecutive days. In the first opening (stage 1), the flowers are functionally female; no pollen is released but the stigma is white and receptive to pollen. The flower then closes until the next day. At the second opening (stage 2), the flower is functionally male; pollen is released and the stigma starts to dry up and turn brown. Each stage lasts 3–4 h. Cultivars are classified according to the time of day that they flower. Type A cultivars have stage 1 flowering in the morning of one day and stage 2 flowering in the afternoon of the next day. Type B cultivars have stage 1 in the afternoon of one day and stage 2 in the morning of the next day.

Cool nights or cloudy mornings can delay opening and closing of morning flowers. This can cause both stage 1 and stage 2 flowers to occur on trees of the same variety in early afternoon. This overlap of flowering stages allows pollen transfer within the same tree or variety. This is called *close*-pollination.

In Israel, avocado competes with other plants for bee pollinators. In early season, the crop competes for nectar-foraging bees primarily with *Citrus* spp. It is the nectar foragers that are the primary pollinators of this unique crop, so this competition with *Citrus* spp. repre-

sents a limiting factor on early fruit-set in avocado (Ish-Am and Eisikowitch, 1998).

Avocado Pollination Requirements

Avocado seems to be at least partially self-fruitful. However, its unusual flowering behaviour and the existence of Type A and Type B plants appear to be elaborate bids for cross-pollination. Avocado production in California is higher in orchards interplanted with different varieties to promote cross-pollination (McGregor, 1976).

Nevertheless, in Florida 30–80% of stigmas stay white and receptive in stage 2 when the flower is releasing pollen; thus, selfing is possible. Moreover, selfing in stage 2 seems to be the rule for most Florida avocado. With individual flowers of varieties 'Hardee' (Type B) and 'Simmonds' (Type A) that were bagged to exclude bees during stages 1 and 2, pollination rates were the same as for open-pollinated flowers. Pollen was transferred from anthers to receptive stigmas inside single stage 2 flowers by wind, gravity, or thrips. Pollination of stage 1 flowers required pollination by flying insects, but pollination rates of

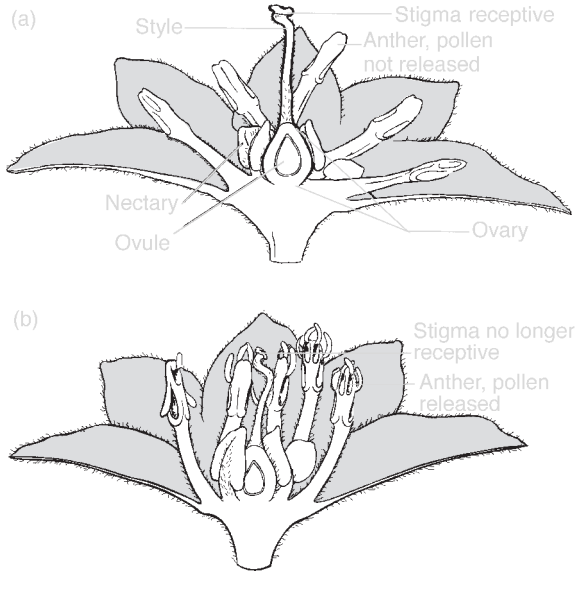


Fig. 19.1. Flower of avocado, *Persea americana*. (a) stage 1, (b) stage 2. (Source: Darrell Rainey.)

open-pollinated stage 1 flowers were only about 1%. Thus, in Florida there seems to be two opportunities for pollination – at stage 1 (by cross-pollinating bees) and at stage 2 (by selfing wind, gravity, or thrips); of these, pollination in stage 2 is the most important (Davenport *et al.*, 1994).

Selfing is not the rule elsewhere, and some varieties are self-incompatible (Stout, 1933; Lesley and Bringhurst, 1951). The high rates of selfing seen by Davenport *et al.* (1994) in Florida may depend on very humid conditions that keep stigmas moist and receptive through stage 2. In drier regions the stigmas must be pollinated during stage 1 while they are receptive which, of course, requires pollen from another plant and a pollinator to transfer it. If stages 1 and 2 overlap on a plant and close-pollination is possible, then insects are necessary to transfer large amounts of pollen. The large, sticky structure of avocado pollen suggests that the plant is well suited for insect pollination and, by inference, cross-pollination. High avocado fruit-set in Israel is correlated with high honey bee activity (Ish-Am and Eisikowitch, 1991). Thus, the plant's flowering biology and grower experience generally favour insect-mediated cross-pollination with compatible Type A and Type B varieties (McGregor, 1976; Free, 1993; Davenport *et al.*, 1994). In ideal cross-pollinating conditions, Type A trees are pollinated with pollen from compatible Type B trees in the morning, and Type B trees are pollinated by Type A trees in the afternoon.

Cool weather is more detrimental for Type B plants than for Type A. If bad weather delays stage 1 bloom in Type A plants until the afternoon, insects are still active and they may pollinate the flowers. However, if Type B plants are delayed, stage 1 may occur so late in the day that insects are no longer active (Peterson, 1956).

One can optimize insect cross-pollination by alternately interplanting trees of compatible Type A and Type B cultivars in the same row. A tree should be no more than 50 ft (15 m) from a tree of a different type (Free, 1993). Solid-block plantings of one cultivar do set fruit in some areas, but this is close-pollination (from overlapping stages 1 and 2) or flower selfing (from receptive stage 2 stigmas).

Avocado Pollinators

In its native Central America, avocado is pollinated by native social bees and wasps. However, honey bees are the most important pollinator elsewhere.

The avocado flower is not perfectly suited to honey bees. Bees have trouble walking on it because it is small, and the nectar and pollen are not highly attractive. Nevertheless, bees readily visit the flowers if better forage is not available. Honey bees successfully pollinate avocado

Table 19.1. Recommended bee densities for avocado.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
2–3 (5–7.5)	McGregor (1976)
0.8–1.2 (2–3)	Free (1993)
0.8–3 (2–7.5)	Williams (1994)
1.8 (4.5)	**Literature average**

and increase fruit-set in Australia (Vithanage, 1988), California (McGregor, 1976), and Israel (Ish-Am and Eisikowitch, 1991).

When a honey bee visits a stage 2 flower, it contacts the anthers at specific sites on its body; pollen remains at these collection sites (also called *safe sites*) and is transferred to stigmas when the bee visits a stage 1 flower. This transfer is easy because the sexual parts of stage 1 and 2 flowers both contact the bee safe sites during a normal bee visit. Nectar-collecting honey bees visit both stage 1 and 2 flowers, whereas pollen-collectors prefer stage 2 flowers (Ish-Am and Eisikowitch, 1993). Therefore, nectar-collecting honey bees are the primary pollinators of avocado.

Because honey bees are easily distracted by competing bloom (Ish-Am and Eisikowitch, 1998), it is advisable to aim for a high density of honey bee colonies in avocado (Table 19.1).

Chapter 20

Bean (Lima)

Flowering

The lima bean (*Phaseolus lunatus*) flower is on the end of a pedicel on a 2–4 in (5–10 cm) raceme. The keel of the legume-type flower is elongated into a twisting beak. Inside the keel are the style, stigma, and the pollen-bearing anthers (Fig. 20.1). Anthers drop pollen on the portion of style below the stigma. When pressure is applied to the flower, as from a visiting bee, the stigma and a portion of the style project out of the keel; they retract when pressure is removed. Pollen from the pollen-dusted style rubs on to the end of the keel and contacts the stigma as it retracts. Cross-pollination is possible if the stigma is pollinated by a bee before it retracts.

Not all flowers on a raceme set fruit. The problem may be high temperature, low humidity, or poor pollination (McGregor, 1976). The lima bean flower produces nectar and pollen, and bees will visit the plant if no richer forages are available.

Lima Bean Pollination Requirements

Both self-pollination and cross-pollination can occur in lima bean. The number of pods, beans per pod, and total weight of beans increase in non-caged plants compared to plants caged to exclude bees; but other studies contradict this. Crossing promotes hybrid vigour in lima bean, but this sometimes happens without the help of bees. Production of hybrid seed increases in the presence of bees. Overall, cross-pollination is rarely necessary, but probably helpful (McGregor, 1976).

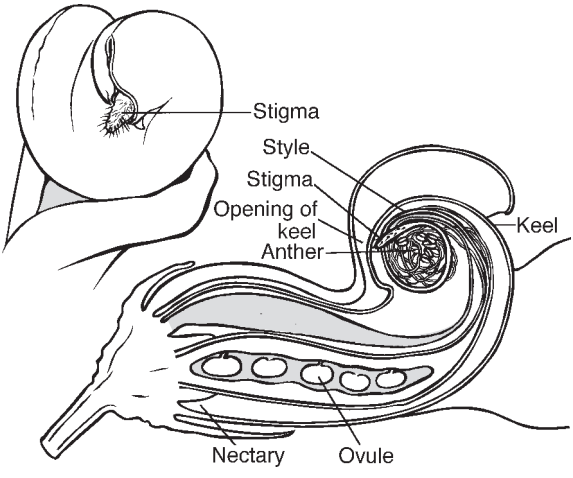


Fig. 20.1. Flower of lima bean, *Phaseolus lunatus.* (Source: Darrell Rainey.)

Lima Bean Pollinators

Honey bees and bumble bees readily visit lima bean and promote cross-pollination. A few studies have credited bees with higher yields (McGregor, 1976). Thrips are numerous in lima bean flowers and may pollinate the flowers; they may even cross-pollinate if crowding forces them to leave one flower and go to another (Free, 1993).

There are few or no research-based recommendations for bee densities in lima bean. However, there is evidence that the presence of bees can only help improve yield. Supplying one honey bee hive per acre (2.5 ha^{-1}) is a prudent measure for optimizing cross-pollination and yields. Additional benefit may be realized by conserving local bumble bee populations by leaving field margins undisturbed and by planting bee pasture plants in order to offset natural dearth periods (see Chapter 8, page 67).

Chapter 21

Bean (Common, Green, Snap)

Flowering

The common bean (*Phaseolus vulgaris*) flower has an elongated, twisted keel containing the style and ten stamens. Inside the flower, the anthers drop pollen on to the style in the evening before it opens. The next day if pressure is applied to the flower, by an insect for example, the style and stigma protrude from the keel and retract when the pressure is released. The style leaves pollen at the opening of the keel. Cross-pollination is possible if the stigma contacts a pollen-coated bee while it is extended. Otherwise, the stigma will be self-pollinated when it retracts and contacts its own pollen at the opening of the keel (McGregor, 1976).

Green Snap Bean Pollination Requirements

Self-pollination is the norm with green snap beans, and it probably happens automatically at or before flower opening in the morning. However, it takes 8–9 h for pollen tubes to grow and fertilize seeds, during which time honey bees and bumble bees can visit the flower and cross-pollinate it. Tubes of foreign pollen probably grow faster than the plant's own pollen, so crossing is likely when the plant is cross-pollinated (Free, 1993). For the grower, there is no yield or other economic advantage to cross-pollination. For the bean breeder, cross-pollination is actually a hazard to maintaining purity of varietal seed. To reduce unwanted hybridizing, one can separate varieties by at least 6–12 ft (1.8–3.7 m) and a tall, dense barrier. With Canadian varieties, it is the practice to separate 'registered' seed stocks by 150 ft (46 m) and 'elite' seed stocks by 0.3 mile (0.5 km) (Free, 1993).

Green Snap Bean Pollinators

Bumble bees visit green snap beans more than do honey bees (McGregor, 1976). However, the overall benefit of bees to green snap bean production is probably small.

Chapter 22

Beet Seed

Flowering

The small, greenish flower of beet (*Beta vulgaris*) occurs on a branched seed stem in clusters of two or three (Fig. 22.1). Flowers are perfect but selfing is rare because stigmas mature later than the anthers. Flowers open in the morning and anthers release pollen before noon. Stigmas begin opening in the afternoon and are not fully open until days 2–3 when the anthers of the same flower are no longer producing pollen. Once open, stigmas may stay receptive for more than two weeks. The pollen is wind-borne. Many insects visit beet flowers. Honey bees visit beet, but they readily move to more attractive food sources.

Beet Pollination Requirements

Beets are generally self-incompatible, and cross-pollination by wind or insects is important. No doubt wind is the most important pollinating agent. Beet pollen has been recovered 2.8 miles (4.5 km) from a crop and 16,393 ft (5000 m) above it (Meier and Artschwager, 1938). Contamination by abundant wind-borne pollen can be a problem in production of certified seed and hybrid varieties that require controlled cross-pollination. Tetraploid plants, used in hybrid seed production, produce fewer and larger pollen grains than diploid plants. Therefore, insect pollination is probably more important for hybrid seed than for normal seed production (Scott and Longden, 1970).

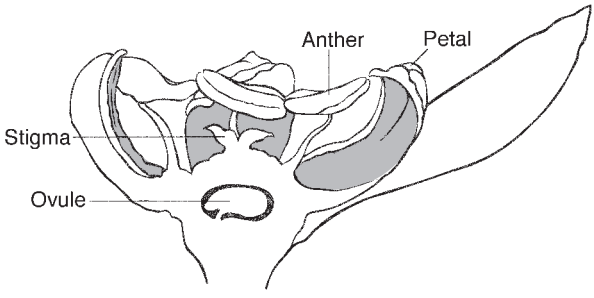


Fig. 22.1. Flower of beet, *Beta vulgaris*. (Source: Darrell Rainey.)

Beet Pollinators

Wind is the major pollinator of beet. Numerous flies, beetles, and bees visit beet flowers. Many of these visitors carry beet pollen and probably help pollination (Free *et al.*, 1975). Honey bee visitation sometimes increases seed yield (Mikitenko, 1959), but their overall contribution to pollination is probably negligible (Aleksyuk, 1981).

Chapter 23

Blackberry

Flowering

The blackberry (*Rubus fruticosus*) flower is whitish, about 1 in (2.5 cm) diameter, and perfect. It has four petals and 50–100 stamens clustered around 50–100 pistils (Fig. 23.1). Each pistil, when fertilized, develops into a succulent drupelet; thus, blackberry is an aggregate fruit. Nectar is excreted at the base of the flower. The nectar and pollen are attractive to bees, and bee-keepers in the southern US and Pacific states often make surplus crops of blackberry honey. Most pollination takes place within the first two days after the flower opens.

Blackberry Pollination Requirements

There are over 400 species of cultivated and wild blackberries in North America; some are self-sterile and need cross-pollination, and others are partially self-fertile. The varieties 'Cory Thornless', 'Flordagrand', and 'Mammoth' are at least partially self-sterile and benefit from cross-pollination. The variety 'Oklawaha' was developed to provide pollen for 'Flordagrand' and itself produces fruit if it is cross-pollinated (McGregor, 1976).

Considering the cross-pollination benefits of wild blackberry, it may be advisable to preserve wild stands in order to provide pollination for nearby commercial plantings. However, wild stands can also harbour pests and diseases.

Regardless of whether a blackberry plant is self-fertile or -sterile, bee pollinators provide the benefit of maximizing the distribution of pollen to all receptive stigmas. This increases the number of developing druplets and size of the fruit, thereby improving its shape.

Table 23.1. Recommended bee densities for blackberry.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
3–4 (7.5–10)	Crane and Walker (1984)
1 (2.5)	Scott-Dupree *et al.* (1995)
2.7 (6.7)	**Literature average**
Other measures	
1 honey bee per 100 flowers	McGregor (1976)

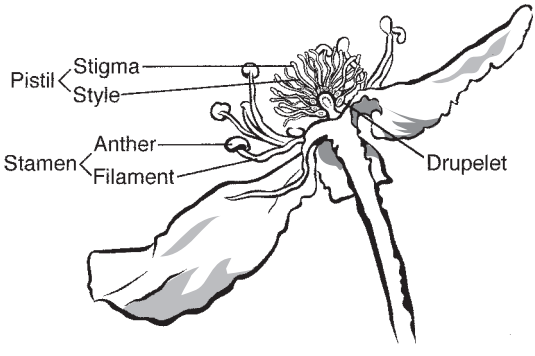


Fig. 23.1. Flower of blackberry, *Rubus fruticosus*. The flower has been partially dissected to reveal interior structures. (Source: (art) Darrell Rainey; (photo) Jim Strawser.)

Blackberry Pollinators

Bees readily visit blackberry, and by pollinating the flower they improve the size and shape of this aggregate fruit. Honey bees sometimes increase yield and speed ripening even in self-fertile varieties, as shown for 'Thornless Evergreen' (Praagh, 1988). Gyan and Woodell (1987) bagged blackberry flowers, removed the bags, noted the first insect visitor, and counted the pollen grains deposited after one insect visit. On average, hover flies deposited 2.1 pollen grains; honey bees deposited 6.4 grains, and bumble bees deposited 8.3 grains. This demonstrates the comparative efficiency of bees as insect pollinators of blackberry (Table 23.1).

Chapter 24

Blueberry

There are three general types of blueberry commercially grown: highbush (*Vaccinium australe*, *V. corymbosum*), lowbush (*V. angustifolium*, *V. myrtilloides*), and rabbiteye (*V. ashei*). Lowbush is a spreading, ground-covering blueberry grown in the northern US and Canada. It develops from a fertilized seed but spreads as a single clone with underground growth to cover a large area. Lowbush blueberry can quickly colonize burned or cleared ground. Highbush and rabbiteye blueberries are upright, individual plants well suited to intense orchard management. Highbush varieties are grown throughout much of Europe and North America; rabbiteye is predominantly grown in the southern US. Genes of northern highbush varieties have been incorporated into southern *Vaccinium* spp. stocks to produce southern highbush varieties that ripen earlier than rabbiteye. Earliness of ripening is important in the premium-priced fresh market.

Flowering

The blueberry flower occurs on racemes along or at the ends of branches. The pinkish-white petals join to form a tubular corolla $\frac{1}{4}$–$\frac{1}{2}$ in (0.6–1.3 cm) long that hangs downward. There are eight to ten stamens at the base of the corolla surrounding a long style that extends beyond the anthers and to the opening of the corolla (Fig. 24.1). The style is receptive to pollen only at the stigma. At the end of each anther is a pore through which pollen is released during the period of stigma receptivity. Nectar is produced at the base of the corolla. Fruit-set is unlikely if the flower is not pollinated within the first 3 days of opening. If the ovary is successfully fertilized, it ripens 2–3 months later into a berry containing up to 65 small seeds.

The flower is well suited to buzz-pollinating bees. When the flower is vibrated by a buzz-pollinator, such as a bumble bee, the

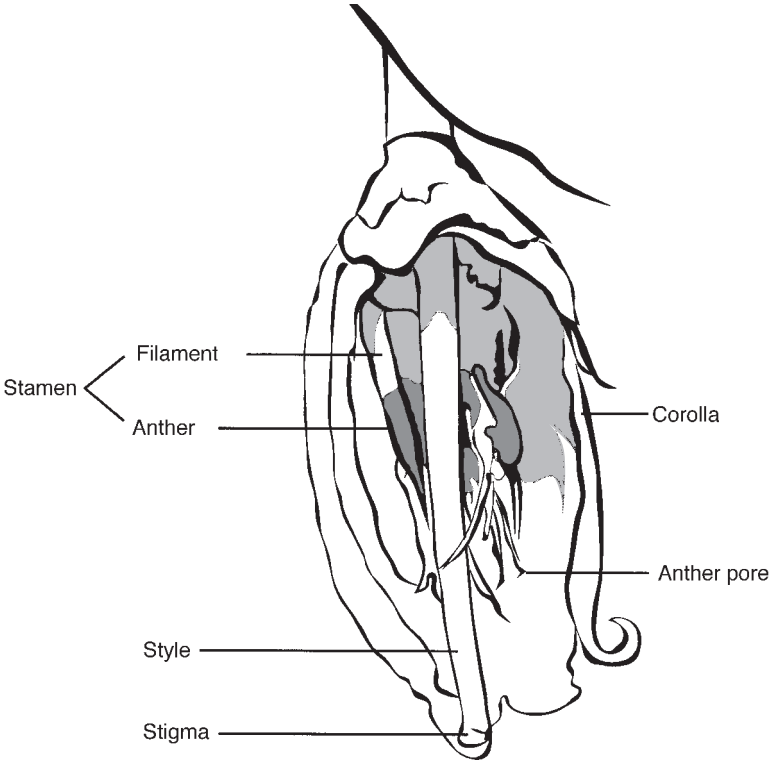


Fig. 24.1. Flower of blueberry, *Vaccinium* species. The flower has been partially dissected to reveal interior structures. (Source: (art) Darrell Rainey; (photo) Jim Strawser.)

pollen falls out of the pollen pores and on to the insect which is usually probing the flower for nectar at the same time. The nectar and pollen are attractive to bees, but the flower morphology makes it difficult for some bees, including honey bees, to legitimately pollinate the flower. Some pollen is released even at slight pressures, and in this manner even non-buzz-pollinators can receive and transport pollen as long as they visit the flower at its opening (McGregor, 1976; Delaplane, 1995). Lyrene (1994) has suggested that short and wide corollae, large corolla apertures, and a short distance between the stigma and anthers are desirable characteristics that could make the blueberry flower more amenable to honey bee pollination. Highbush varieties can possess some of these characteristics, but the flower morphology of rabbiteye (*V. ashei*) is especially problematic for honey bees because the corollae tend to be comparatively long, the corolla apertures narrow, and the distance between anthers and stigma large (Ritzinger and Lyrene, 1999). One breeding study has shown that F_1 hybrids between *V. ashei* and a wild species expressing desirable flower characteristics, *V. constablaei,* exhibit flower characteristics generally intermediate between the two (Ritzinger and Lyrene, 1999). Thus, it may be possible to use *V. constablaei* to breed for varieties of *V. ashei* that are more attractive to honey bees.

Some bees, especially carpenter bees (Chapter 13), rob blueberry flowers by cutting slits in the corolla to reach nectar and completely bypassing the sexual parts. These flower visits probably do not result in pollination. On average, the percentage of *Vaccinium* spp. pollen in pollen loads of foraging bees is higher with legitimate flower visitors (77.7%) than with robbers (47%) (Delaplane, 1995).

Blueberry Pollination Requirements

In general, lowbush and highbush varieties range from moderately self-sterile to self-fertile. Almost all rabbiteye varieties are self-sterile and require cross-pollination. All types benefit from a high number of fertilized seeds per berry which improves fruit-set, increases berry size, and speeds ripening. Thus, bee activity is important for transporting pollen to receptive stigmas even in self-fertile varieties. Eck (1988) estimates that 60–80% of blueberry flowers must set fruit in order to achieve a commercially viable yield.

Lowbush pollination requirements

Lowbush blueberry clones range from self-sterile to moderately self-fertile (Hall and Aalders, 1961). Cross-pollination generally improves

fruit-set in *V. angustifolium* (Wood, 1968). The two main lowbush species *V. angustifolium* and *V. myrtilloides* often grow together naturally in cleared lands. The two occur in about equal proportions in cleared forest, whereas *V. angustifolium* predominates in abandoned farmland. The berries abort when *V. angustifolium* is pollinated with pollen from *V. myrtilloides*. Therefore, one can expect a maximum fruit-set of about 50% in cleared forest where the two species occur. Fruit-set can be much higher in patches where *V. angustifolium* predominates. There would be probably fewer pollination problems in lowbush blueberry if plantings could be restricted to two or more good pollen-producing clones of the same species (Hall and Aalders, 1961). With *V. angustifolium*, over 5% of the plants are male-sterile and 45% produce relatively little pollen (Hall and Aalders, 1961). Thus, pollen scarcity can be a limiting factor in production, and this necessitates good pollinator activity in order to move the available pollen among plants.

Highbush pollination requirements

Highbush varieties are largely self-fertile (El-Agamy *et al.*, 1979), but cross-pollination sometimes increases number of seeds per berry, fruit-set, fruit size, and speed of ripening. Honey-bee-mediated cross-pollination of the southern highbush variety 'Sharpblue' (with 'Gulfcoast') increased yield of early-ripening 'Sharpblue' fruits by 140%, increased heavy (≥ 0.75 g) fruits by 13%, and decreased small fruits by 66%, all of which translated to a 43% increase in early-market crop value – about US$2000 acre^{-1} (US$5000 ha^{-1}) (Lang and Danka, 1991). Cross-pollination did not affect fruit-set. However, fruit-set in 'Sharpblue' crossed with *V. corymbosum* clones 'O'Neal' and 'FL 2–1' was at least twice as high as in selfed plants; moreover, cross-pollination increased the number of seeds per berry and speed of ripening (Lyrene, 1989). Fruit-set was lowest in selfed 'Sharpblue', intermediate in 'Sharpblue' and a 'Sharpblue' + 'FL 2–1' mixture, and highest in 'Sharpblue' + 'FL 2–1' alone, demonstrating a degree of self non-fruitfulness in 'Sharpblue'. Congruent results were found by Huang *et al.* (1997) who demonstrated that crossing 'Sharpblue' with 'O'Neal' or with 'Gulfcoast' reduced the incidence of poorly-developed ovules, reduced incidence of ovule abortion, and increased fruit mass at ripening compared to selfed 'Sharpblue'.

Gupton and Spiers (1994) showed that varieties perform differently as pollen donors, that is have different effects on development of the berry. In crossing experiments with seven southern highbush varieties, selfing generally did not affect fruit-set, but it reduced number of seeds per berry, berry weight, and speed of ripening, thus confirm-

ing earlier studies. Pollens from 'Georgiagem' and 'Cape Fear' generally produced the longest ripening times in the main variety, and 'O'Neal' and 'Gulfcoast' pollens produced the shortest ripening time. Pollens from 'Blue Ridge', 'Gulf Coast', and 'O'Neal' produced the heaviest berries in the main variety.

Pollinating southern highbush varieties with pollen from rabbiteye varieties does not affect fruit-set and speed of ripening, but it reduces number of seeds per berry and berry weight (Gupton and Spiers, 1994).

Solid-block plantings of southern highbush varieties, especially 'Sharpblue', are common, but based on these studies growers may benefit from interplanting highbush blueberries with compatible highbush pollenizers. Speed of ripening, and consequently cross-pollination, are less important in areas where highbush blueberries are grown for processing. Solid-block plantings may give satisfactory results in these cases.

A two-year study in New York established the pollination requirements of three northern highbush varieties (MacKenzie, 1997). With the variety 'Bluecrop', cross-pollination (with 'Spartan', 'Coville', or 'Patriot') conferred little benefit over selfing. For 'Northland', the fruit-set was unacceptably poor (≤ 20%) when flowers were bagged to exclude pollinators, and in 1 year of the trial cross-pollination (with Coville) improved fruit weight, seed number, and speed of ripening over self-pollination or open pollination. In the variety 'Patriot', cross-pollination (with 'Spartan', 'Coville', or 'Bluecrop') increased the number of viable seeds compared to open pollination or selfing; cross-pollination (with 'Spartan' or 'Coville') also increased fruit weight in one year compared to open pollination, and crossing in the second year (with 'Bluecrop') improved fruit weight and speed of ripening compared to selfing. The three varieties also differed in the degree of expressed parthenocarpy. 'Northland' yielded only two seedless berries while 'Patriot' had significantly more seedless berries (58%) than 'Bluecrop' (20%).

Rabbiteye pollination requirements

Rabbiteye varieties are largely self-sterile and require cross-pollination with a suitable rabbiteye variety (El-Agamy *et al.*, 1979). One exception to this is the variety 'Centurion', which is self-fertile at least when grown in North Carolina (P. Lyrene, Univ. Florida, personal communication). But the general rule is that cross-pollination with other rabbiteye varieties improves fruit-set, size, and earliness of ripening. Pollinating rabbiteye with pollen from southern highbush, on the other hand, reduces fruit-set, number of seeds per

berry, berry weight, and speed of ripening in rabbiteye (Gupton and Spiers, 1994).

If one selects rabbiteye varieties carefully for orchard interplanting, it is possible to provide bloom overlap of compatible varieties for good cross-pollination and thus prolong the harvest season. It is important to select varieties for interplanting that have similar chill hour requirements (that is, winter hours below 45°F (7.2°C)) because these varieties have the most bloom overlap. Table 24.1 describes characteristics of some rabbiteye varieties widely used in the southern US.

Information provided in Table 24.1 can help one select rabbiteye varieties for interplanting. For example, an interplanting of 'Beckyblue', 'Bonita', and 'Woodard', having similar chill hours, would promote good bloom overlap and cross-pollination. By interplanting 'Climax', 'Bluebelle', and 'Baldwin', one could maximize both cross-pollination and length of harvest interval. Many other factors must enter the decision making process, however, including varietal differences in flavour and harvesting properties, as well as pollen compatibility. Extension agents and crop advisers are valuable resources for determining the best varietal blend for a particular area.

The planting arrangement of rabbiteye blueberries is important to good cross-pollination (Krewer *et al.*, 1986). The goal is to increase the chance of a bee visiting two or more varieties during the same foraging trip. If the objective is to grow equal numbers of two varieties, they can be planted according to plan 1 (Fig. 24.2). If the goal is two-thirds

Fig. 24.2. Plan 1 orchard design for encouraging cross-pollination in rabbiteye blueberry. There are equal numbers of two varieties. (Source: Carol Ness.)

Table 24.1. Rabbiteye blueberry varieties (from Krewer *et al.,* 1986 and 1993).

Variety	Chill-hour requirement	Spring freeze resistant?
	Early-season harvest	
Beckyblue	300	
Bonita	300	
Brightwell	350–400	✓
Climax	450–550	
Premier	550	
Woodard	350–400	
	Mid-season harvest	
Bluebell	450–500	
Briteblue	400–650	
Powderblue	550–650	✓
Tifblue	550–750	✓
	Late-season harvest	
Baldwin	450–500	
Centurion	550–650	✓
Delite	500	

of variety A and one-third of variety B, they can be planted according to plan 2 (Fig. 24.3). For three varieties, plan 3 is an appropriate model (Fig. 24.4).

Growers in the southern US perceive that pollination is a limiting factor in rabbiteye blueberry production. One problem is the morphology of the flower which is not conducive to pollination by honey bees, the most abundant pollinator (Ritzinger and Lyrene, 1999) (see page

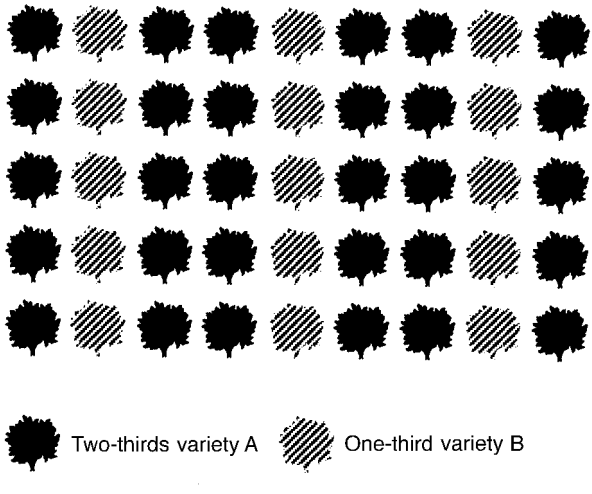


Fig. 24.3. Plan 2 calls for two-thirds of variety A and one-third of variety B. (Source: Carol Ness.)

Fig. 24.4. Plan 3 calls for equal numbers of three varieties. (Source: Carol Ness.)

171). Another is the regular risk of freeze damage during the critical spring pollination window. NeSmith *et al.* (1999) chilled plants of 'Brightwell' and 'Tifblue' at 32, 30.2, 26.6, or 23.9°F (0, −1, −3, or −4.5°C) for one hour during flowering and then exposed the plants to pollination by either bumble bees only or to bees plus the growth regulator gibberellic acid (GA_3). Fruit-set in the bee pollination treatment dropped sharply in plants chilled to 30.2°F (−1°C) or lower, but fruit-set in the bees plus GA_3 treated plants did not decline significantly from non-chilled controls until temperatures dropped below 26.6°F (−3°C). Thus, GA_3 confers some degree of compensation for chill-induced pollination deficiencies. GA_3 has become widely used in the southern US, but it should not be thought of as a replacement for pollination. Compared to hand pollinated plants, fruit weight was lower and time to ripening longer in 'Beckyblue' rabbiteye plants treated with GA_3 only, and fruit weight was maximized when GA_3 was used in conjunction with pollination (Cano-Medrano and Darnell, 1998). Thus, GA_3 treatment is best thought of as a pollination supplement or compensation for periods of suboptimal pollination conditions.

Blueberry Pollinators

The blueberry flower is well suited for buzz-pollinators, that is, bees that are able to vibrate the flower rapidly to release pollen through the pores in the anthers. Buzzing, or sonicating, greatly increases the amount of pollen released by the flower and falling on to the bee, and

the relative efficiency of single bee visits depends largely on whether that species can buzz-pollinate. But even non-buzz-pollinating species, such as honey bees, can pollinate blueberry when they are present in sufficient numbers and visit flowers legitimately.

Lowbush blueberry pollinators

Honey bees and many species of non-managed bees visit lowbush blueberry (Table 24.2). Some wild bees are locally numerous and probably important pollinators. This seems to be the case for *Andrena carlini*, *A. carolina*, *A. vicina*, *Evylaeus quebecense* [sic], *Dialictus viridatus*, *Bombus perplexus*, *B. ternarius*, and *B. terricola* in Nova Scotia (Finnamore and Neary, 1978) and for *D. pilosus pilosus*, *E. quebecensis*, *B. ternarius*, and *B. terricola* in Sagamie, Québec (Morrissette *et al.*, 1985). Populations of wild bees are generally too small or unpredictable to support commercial pollination needs in lowbush blueberry (Morrissette *et al.*, 1985).

Wild pollinators can be supplemented with honey bees. Yield in Newfoundland lowbush blueberry fields stocked with honey bees at 0.7 colonies acre^{-1} (1.7 ha^{-1}) was 54% higher than in fields without supplemental honey bee hives (Lomond and Larson, 1983). In Québec, 500 honey bee hives were introduced during bloom at one end of a large lowbush blueberry farm, and researchers measured bee densities and fruit characteristics at regular intervals in the field for up to 3.1 miles (5 km) from the hives (Aras *et al.*, 1996). Honey bee densities decreased as distance from the hives increased. As honey bee densities decreased, there was a corresponding drop in seed set, fruit-set, berry weight, and speed of fruit ripening. Densities of wild non-honey bees were uniform across the field; thus, these results demonstrate the contribution of honey bees to lowbush blueberry pollination.

Positive results from importing honey bees may stem in part from the particular mixture of lowbush species *Vaccinium angustifolium* and *V. myrtilloides* growing in a field. When *V. angustifolium* and *V. myrtilloides* occur together, incompatibility problems can limit maximum fruit-set to about 50% (Hall and Aalders, 1961). But where *V. angustifolium* predominates, incompatibility is not a problem and the fruit-set potential and the potential value of honey bees are much higher (Free, 1993).

Managed leafcutting bees and orchard bees may be potential pollinators of lowbush blueberry. Alfalfa leafcutting bees (Chapter 11) and the orchard bee *O. ribifloris* (Chapter 12) were released in a lowbush blueberry orchard in Maine. Both bee species visited the flowering crop and collected blueberry pollen. However, *O. ribifloris* collected blueberry pollen exclusively and adults emerged in good synchrony

Table 24.2. Non-honey bee pollinators of lowbush blueberry (after Finnamore and Neary, 1978 and Morrissette *et al.*, 1985).

Colletidae	
Colletes consors mesocopus Swenk	*Hylaeus modestus modestus* Say
Colletes inaequalis Say	
Andrenidae	
Andrena algida Smith	*Andrena kalmia* Atwood
Andrena bipunctata Cresson	*Andrena lata* Viereck
Andrena bradleyi Viereck	*Andrena miserabilis bipunctata* Cresson
Andrena carlini Cockerell	*Andrena nivalis* Smith
Andrena carolina Viereck	*Andrena planida placida* Smith
Andrena ceanothi Viereck	*Andrena regularis* Malloch
Andrena clarkella (Kirby)	*Andrena rufosignata* Cockerell
Andrena crataegi Robertson	*Andrena sigmundi* Cockerell
Andrena cressonii Robertson	*Andrena thaspii* Graenicher
Andrena frigida Smith	*Andrena vicina* Smith
Andrena grandior Cockerell	*Andrena wilkella* (Kirby)
Halictidae	
Halictus confusus Smith	*Dialictus cressonii* (Robertson)
Halictus rubicundus (Christ)	*Dialictus disabanci* Knerer & Atwood
Lasioglossum athabascence (Sandhouse)	*Dialictus imitatus* (Smith)
Lasioglossum forbesii (Robertson)	*Dialictus pilosus pilosus* (Smith)
Evylaeus arcuatus (Robertson)	*Dialictus viridatus* (Lovell)
Evylaeus cinctipes (Provancher)	*Augochlora pura pura* (Say)
Evylaeus comagenensis Knerer and Atwood	*Augochlorella striata* (Provancher)
Evylaeus divergens (Lovell)	*Sphecodes cressoni* (Robertson)
Evylaeus foxii Robertson	*Sphecodes persimilis* Lovell & Cockerell
Evylaeus macoupinensis Robertson	*Sphecodes ranunculi* Robertson
Evylaeus quebecensis (Crawford)	*Sphecodes solinis* Graenicher
Megachilidae	
Megachile melanophoea Smith	*Osmia inspergens* Lovell & Cockerell
Osmia atriventris Cresson	*Osmia proxima* Cresson
Osmia inermis (Zetterstedt)	*Osmia tersula* Cockerell
Anthophoridae (see Roig-Alsina and Michener, 1993)	
Nomada cressonii Robertson	*Nomada lepida* Cresson
Apidae: Bombinae	
Bombus borealis Kirby	*Bombus terricola* Kirby
Bombus fervidus (Fabricius)	*Bombus vagans vagans* Smith
Bombus rufocinctus Cresson	*Psithyrus ashtoni* (Cresson)
Bombus perplexus Cresson	*Psithyrus fernaldae* Franklin
Bombus sandersoni Franklin	*Psithyrus insularis* (Smith)
Bombus ternarius Say	

with crop bloom. Leafcutting bees visited the crop, but they were more likely to visit competing bloom (Stubbs *et al.*, 1994).

A separate study demonstrated promising performance of alfalfa leafcutting bees in lowbush blueberry grown in Maine (Stubbs and Drummond, 1997). Fruit-set was increased significantly in most cases in plots nearer to the bee shelters. Alfalfa leafcutting bees increased fruit-set as much as 30% over background pollination provided by honey bees and wild bees. Rate of reproduction, however, was less than 0.2 loose cells per loose cell incubated. If these bees are to be used for commercial pollination of lowbush blueberry, it is probable that cells would have to be purchased annually.

Highbush blueberry pollinators

Although northern and southern highbush varieties range from somewhat self-fertile to highly self-fertile, cross-pollination between many varieties improves fruit size, seed count, and earliness of ripening, all of which are important economic considerations (Lang and Danka, 1991). Large bee populations help transport large quantities of pollen and cross-pollinate highbush blueberry. In one study, honey bee visitation to 'Gulfcoast' highbush variety increased speed of fruit ripening by five days and berry weight by 28%. These effects did not depend on the type of pollen the bees were carrying (selfing with same variety, crossing with different variety, or crossing with a rabbiteye variety), so this study confirms the value of honey bees as pollinators of southern highbush blueberries (Danka *et al.*, 1993b).

With the northern highbush 'Bluecrop', increasing honey bee visitation with a synthetic queen mandibular pheromone (QMP) attractant increased fruit yield by at least 6% and farmgate revenue an average of US$364 acre^{-1} (US$900 ha^{-1}) (Currie *et al.*, 1992a).

Solitary bees may be helpful highbush blueberry pollinators. The orchard bee *O. ribifloris* (Chapter 12) is an efficient pollinator in California highbush blueberry. As few as 300 nesting *O. ribifloris* females can pollinate 1 acre of highbush blueberry (741 ha^{-1}) (Torchio, 1990b). The solitary soil nester *Colletes validus* visits blueberry (many species, including highbush) in Maryland, works the blossoms legitimately, and nests in synchrony with crop bloom. It is a prime candidate for conservation efforts (Batra, 1980).

Rabbiteye blueberry pollinators

Southeastern blueberry bees and bumble bees are the most efficient pollinators of rabbiteye blueberry, based on single-bee flower visits

(Cane and Payne, 1990). The southeastern blueberry bee (*Habropoda laboriosa*) (Chapter 10) emerges, mates, and nests in February–April in close synchrony with blueberry bloom in the southeastern US. These bees appear to be near-obligate specialists on blueberry, and they are sometimes present in blueberry orchards in the southeastern US at economically important pollinating levels (Cane, 1993, 1994; Cane and Payne, 1988, 1991, 1993).

Bumble bees (Chapter 8), especially nesting queens, are naturally plentiful in some rabbiteye orchards in the southeastern US. However, their populations in early spring when rabbiteye is blooming are limited to nesting queens or to very small, young colonies with only a few workers. Thus, the species' maximum forager potential is not realized in time for rabbiteye bloom in that area. Some growers buy commercially-reared mature colonies with ≥ 80 workers each (see Chapter 8, page 82) and disperse them throughout the orchards. However, the efficacy of this practice is untested.

Carpenter bees (Chapter 13) rob rabbiteye blueberry flowers by cutting slits in the side of the flower to reach nectar without touching the anthers or stigma. The robbery holes can then attract other bee species which would otherwise legitimately visit the flower. As few as one carpenter bee per 25 bushes or 4% incidence of slitted flowers can make 80–90% of the honey bees switch to robbing (Cane and Payne, 1991). Whenever possible, blueberry growers should control carpenter bee populations. It may help to remove any piles of lumber that are near the orchard that could provide nest sites for carpenter

Table 24.3. Recommended bee densities for blueberry.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
1, 5, 10 (2.5, 12, 25)	McGregor (1976)
2–5 (5–12)	McCutcheon (1983)
1 (2.5)	Krewer *et al.* (1986)
3–4 (7.4–10)	Levin (1986)
2 (5)	Kevan (1988)
0.5, 0.8, 2 (1.2, 2, 5)	Free (1993)
4 (10)	Williams (1994)
1–4 (2.5–10)	Scott-Dupree *et al.* (1995)
3 (7.5)	**Literature average**
Other bees	
300 *O. ribifloris* females acre^{-1} (741 ha^{-1})	Torchio (1990b)
1–4 bumble bees or southeastern blueberry bees per bush	Cane (1993)
20,000 alfalfa leafcutting bees acre^{-1} (49,420 ha^{-1})	Stubbs and Drummond (1997)

bees. If bees are nesting in wooden sheds, one can control them by injecting an approved insecticide inside individual tunnels, plugging the holes, and painting the wood surfaces.

Honey bees are the most numerous bee visitor in blooming rabbiteye blueberry in south Georgia, USA, followed in descending order by bumble bee queens, bumble bee workers, carpenter bees, and southeastern blueberry bees. Percentage of bees collecting pollen is highest with bumble bee workers (76.3%), followed by southeastern blueberry bees (60%), bumble bee queens (38%), honey bees (3.2%), and carpenter bees (1%). Bumble bee queens and workers carry the highest percentage (70.2%) of *Vaccinium* spp. pollen on their bodies, followed by honey bees (67.7%), southeastern blueberry bees (58.1%), and carpenter bees (29.5%). Thus, bumble bees and southeastern blueberry bees are more diligent pollen collectors in rabbiteye blueberry, but even honey bees and carpenter bees can carry *Vaccinium* spp. pollen on their bodies (Delaplane, 1995).

Chapter 25

Cabbage and Other Crucifer Seeds

This chapter covers the crucifers (*Brassica oleracea*) or cole crops – cabbage, cauliflower, broccoli, Brussels sprouts, kohlrabi, and the kales. Other *Brassica* species, oilseed rape or canola, are covered in Chapter 26. Cole crops are large-leaved, low-growing plants until the time at which they begin flowering. Most are biennial, with the exception of cauliflower which is annual.

Flowering

The flowering stem elongates after leafy growth stops. The stem has many branches, small leaves, and bright yellow or white flowers. Each flower has four petals, ½–1 in (1.3–2.5 cm) long, that form a cross, hence the family name Cruciferae ('cross bearing'). Each flower has six stamens; two are shorter than the style and four are longer. There is a single stigma at the tip of the style (Fig. 25.1). The flower opens in the morning, but the anthers do not release pollen until a few hours later. Nectar is excreted at the bases of the short stamens and ovary. The flower is open for three days, and bees visit the blossoms for nectar and pollen.

Crucifer Pollination Requirements

Crucifers as a group require cross-pollination 95% of the time although some cauliflower varieties are self-fruitful. Many plants are self-incompatible, and some are cross-incompatible. Selfing in the absence of cross-pollination generally reduces seed yield, seed size, and yield in subsequent generations (McGregor, 1976). Wind is not a good pollinator in *Brassica* spp. except in canola (Chapter 26), so bees play an important role in moving pollen. This is especially true in

Table 25.1. Recommended bee densities for crucifers.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
Open seed production	
2–4 (5–10)	McGregor (1976)
1 (2.5)	Mayer (1986)
2 (5)	**Literature average**
Hybrid seed production	
2 (5)	Mayer (1986)

hybrid seed production in which many parent stocks are male-sterile and seed production depends on insects moving viable pollen from male-fertile to male-sterile plants.

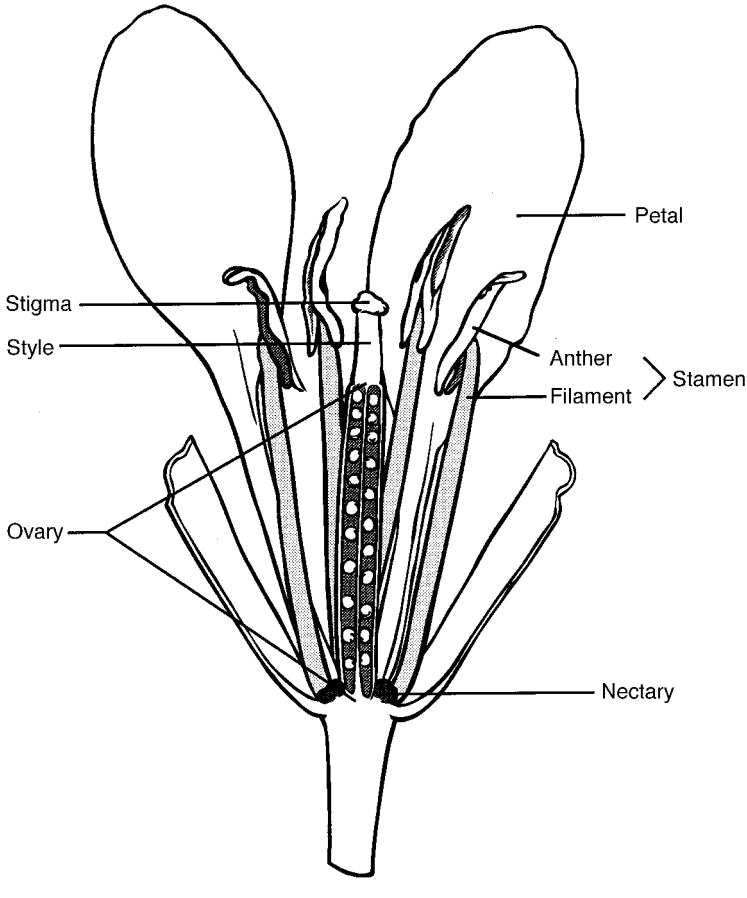


Fig. 25.1. General design of crucifer flowers, *Brassica oleracea*. (Source: Darrell Rainey.)

Crucifer Pollinators

Cabbage flowers are easily accessible to insects, and many types of flies and bees visit them. Non-managed bees are probably important pollinators when they occur in large numbers, especially in cooler temperatures when honey bees are less likely to fly. In general, honey bees are the primary pollinator of crucifers, making up, on average, 84–100% of the pollinators in a field (McGregor, 1976). Pollination and yield are optimized when flowers receive multiple bee visits over several days; this is best achieved by providing large numbers of pollinators (Mayer, 1986).

Honey bee colonies should be brought in when there is enough bloom to attract bees. Bees tend to work down rows, and it is important in hybrid seed production for bees to cross rows and work both male and female plants. Thus, it is advisable to place colonies so that bees leaving the hive are encouraged to forage across rows.

It is important that bees do not discriminate between male and female rows in hybrid seed production. If they prefer one line over the other, they will concentrate on the preferred rows and be less apt to cross-pollinate the crop. This problem can be minimized by making sure that male and female lines have the same height, same flower colour, and bloom at the same time.

Chapter 26

Canola Seed (Oilseed Rape)

Oilseed rape is comprised of two species of *Brassica* – field mustard, sarson, turnip rape, or Polish rape *B. campestris* and Argentine or Swede rape *B. napus*. Rapeseed oil is naturally high in erucic acid and rapeseed meal is high in glucosinolates, both of which have limited the use of rapeseed products in human and animal food. However, plant breeders have developed low-acid, low-glucosinolate varieties (called 'double-low') that are entirely suitable for food. The North American name for double-low varieties, 'canola', is an acronym for 'Canadian oil, low-acid'. *B. campestris* and *B. napus* are grown in Europe, Canada, and northern US states. Almost all oilseed rape grown in the southern US is *B. napus*.

Flowering

The brilliant yellow canola flower grows on a terminal raceme. It has four cruciferous petals, a central style, six stamens (four longer than the style, two shorter), and four nectaries (Fig. 26.1). Flowers may open at any time of day. In *B. napus* the stigma is mature when the flower opens, but the anthers are not yet functional. But before the corolla fully expands, the four long stamens bend away from the style and release pollen. Anthers on the two short stamens release pollen below the stigma. When the flower is old the long stamens bend towards the style, and self-pollination can happen if the plant is self-compatible. Thus, the flower's behaviour and morphology encourage cross-pollination at first, but self-pollination later. Flowering lasts 22–45 days (McGregor, 1976). Oilseed rape is one of the most important honey plants in Canada and the UK. Honey yield potential in Europe can range from 90 to 450 lb acre^{-1} (100–500 kg ha^{-1}) (Williams, 1980). Bee-keepers in the southern US get about 35–70 lb (16–32 kg) per hive.

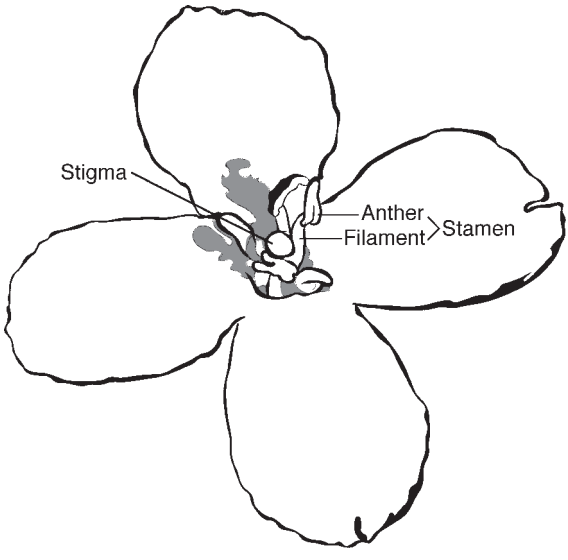


Fig. 26.1. Flower of canola (oilseed rape), *Brassica napus*. (Source: (art) Darrell Rainey; (photo) Jim Strawser.)

Canola Pollination Requirements

In general, *B. campestris* benefits from cross-pollination and *B. napus* is self-fertile.

With the *B. campestris* varieties 'Torch' and 'Span', it was found that pod set, number of seeds per pod, and weight of seed per plant

are higher in cross-pollinated plants than in selfed plants (Williams, 1978). Insects are important cross-pollinators in *B. campestris;* per cent pod set, seed yield, seed weight, speed of ripening, and oil yield are higher when insect pollination is optimized (Langridge and Goodman, 1975; Fries and Stark, 1983; Holm *et al.*, 1985; Mishra *et al.*, 1988; Singh and Singh, 1992). The yellow-seeded varieties 'Sampad', 'Sampad-1', 'Sonali', and 'M-91' are apparently self-fertile, but they do not self-pollinate effectively (Holm *et al.*, 1985). Overall, it is in the grower's best interest to encourage large bee populations in fields of *B. campestris*.

Brassica napus varieties 'Erglu', 'Gulle', 'Janetskis', 'Maris Haplona', 'Midas', 'Oro', 'Turret', and 'Zephyr' are self-fertile, and seed set is good whether the plant is selfed or cross-pollinated. Varieties 'Erglu' and 'Turret' have slightly more seeds per pod when they are cross-pollinated. Even though 'Gulle' is self-fertile, hand-pollinating increases set of early flowers; this suggests that supplemental pollination (such as honey bee hives) may increase set of early flowers, evenness of ripening, and ease of harvest (Williams, 1978). Although *B. napus* is self-fertile, it does not always self-pollinate (Eisikowitch, 1981); thus insects are important for moving pollen from anthers to stigmas. In *B. napus*, there is evidence that most of the pollen moved by bees from any particular plant is deposited on to immediate neighbouring plants, but it is possible that pollen dispersal may extend as far as 40 intervening plants away from the originating one (Cresswell *et al.*, 1995).

Anthers of oilseed rape release pollen when the flowers are shaken, whether by wind or insects. This shaking is very important to rape pollination; plants grown in still, insect-free cages typically have poor seed set (Eisikowitch, 1981; Mesquida and Renard, 1982; Mesquida *et al.*, 1988). Plots exposed to wind but caged to exclude insects often yield at least as well as open-pollinated plots (Free and Nuttall, 1968; Langridge and Goodman, 1982). However, the pollen grains are sticky like most insect-borne pollens, and insects are helpful supplemental pollinators.

In Europe there has been concern that edible double-low rapeseed could become contaminated with pollen from high erucic acid varieties grown on set-aside land. This contamination could result in part from wind- or insect-mediated pollination. EU standards require that rapeseed harvested for human consumption contains less than 2% erucic acid. In a field trial in the UK (Bilsborrow *et al.*, 1998), plots of double-low and high-acid rapeseed were grown next to each other. Resulting seeds were then collected from throughout the double-low plots and analysed for erucic acid content. Erucic acid concentrations ranged from 0 to 9.9%, but at most only 4% of the sampled areas contained acid levels of 2% or higher. It was

judged that contamination of edible rapeseed is not a serious risk, especially at field-scale cultivation.

Canola Pollinators

Canola is extremely attractive to bees. In Georgia, about 63.8% of bee visitors to canola are honey bees; 23.8% are carpenter bees; 7.5% are bumble bees, and 5% are other bees (K.S. Delaplane, unpublished data). Oilseed rape is also visited by many flies, butterflies, and true bugs (Hemiptera); however, pollen loads are usually higher on bee visitors (Williams, 1985).

Most bee visitors can pollinate canola, whether they are collecting pollen or nectar. When honey bees probe rape flowers legitimately they transfer pollen to stigmas (Free and Nuttall, 1968; Eisikowitch, 1981). However, honey bees sometimes rob the flowers without pollinating them. In *B. napus*, 18–65% of the honey bee nectar-collecting visits are robberies (Mohr and Jay, 1988). Overall however, honey bees touch the stigmas of 75% of the flowers they visit (Free and Nuttall, 1968). Bumble bees also transfer pollen to stigmas and, compared to other bees, are less discouraged by inclement weather (Eisikowitch, 1981). Alfalfa leafcutting bees effectively pollinate *B. campestris* in glasshouses (Holm *et al.*, 1985).

B. campestris and *B. napus* may differ in their attractiveness to honey bees. The total number of insect pollinators in France was the same between *B. campestris* and *B. napus*, but honey bee density was 3–7 times higher in *B. campestris*. The distribution of bumble bees and solitary bees was not different between the two rapeseeds (Brunel *et al.*, 1994). However, honey bees showed no preferences in Canada among *B. campestris* varieties 'Candle' and 'Tobin' and *B. napus* varieties 'Altex', 'Andor', and 'Regent' (Mohr and Jay, 1990).

Bees are managed for pollination in hybrid canola seed production in Canada; however, few oilseed canola growers manage bees for pollination. Nevertheless, bees can improve yields (as in *B. campestris*) or help transfer pollen in self-fertile canola (as in *B. napus*). Since bees can only help, growers should do nothing to reduce bee populations such as apply insecticide while canola is blooming.

Insecticide sprays during bloom can devastate local bee populations because rape is a rich and highly attractive bee forage. For example, bee kills on rape were high from applications of triazophos to control cabbage seed weevil and brassica pod midge in England and Wales in the late 1970s. In response to this problem, the Ministry of Agriculture, Fisheries, and Food restricted triazophos treatments to ground applications after 90% petal fall. By 1991, bee kills had

Table 26.1. Recommended bee densities for canola (oilseed rape).

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
1–2 (2.5–5)	McGregor (1976)
For turnip rape, *B. campestris*	
0.8 (2)	Langridge and Goodman (1975)
1.2–1.6 (3–4)	Kevan (1988)
1–6 (2.5–15)	Scott-Dupree *et al.* (1995)
2 (5)	**Literature average**

declined even though rapeseed acreage had expanded rapidly (Greig-Smith *et al.*, 1994). This case history illustrates that sometimes a small change in pesticide application technique can permit a pest to be controlled without destroying beneficial organisms.

Chapter 27

Cantaloupe

Flowering

A single cantaloupe (*Cucumis melo*) plant has perfect flowers and imperfect (male only) flowers. Flowers are $\frac{3}{4}$–$1\frac{1}{2}$ in (2–3.8 cm) across; each has five petals joined as a tube at the base then spreading to form an outer whorl (Fig. 27.1). The perfect flower has anthers and a three-lobed stigma surrounded by nectaries. The imperfect male flower has five stamens, two pairs of which are united; at the base of the corolla there is a non-functioning style surrounded by nectaries. Male flowers usually outnumber perfect flowers 12 to 1; however, if fruit-set is poor the plant may compensate by producing a higher proportion of perfect flowers. Flowers open shortly after sunrise and close in the afternoon of the same day. The stigma is receptive to pollen for only a few hours in the morning, but in hot weather the stigma may be receptive for only a few minutes. Therefore, good bee visitation in early morning is important to fruit-set. Bees visit cantaloupe blossoms for pollen and nectar.

Cantaloupe Pollination Requirements

Cantaloupe is self-fertile, but the perfect flowers cannot self-pollinate. At least 400 seeds must set in order to produce a marketable fruit; accordingly, each stigma must receive at least 400 pollen grains (Bohn and Davis, 1964). This transfer must be done by insects because the pollen is too heavy for wind transport. Although the plant is self-fruitful, cross-pollination slightly increases fruit weight (McGregor, 1976).

Cantaloupe Pollinators

Honey bees are commonly used to pollinate cantaloupe in North America (McGregor, 1976), Israel (Dag and Eisikowitch, 1995), and West Africa (Vaissière and Froissart, 1996), although ants, thrips, and beetles will also visit the flowers.

Increasing the density and dispersal of honey bee hives in the field improves yield, weight, and sweetness of 'Primo' variety cantaloupe. In an experiment in the lower Rio Grande valley of Texas, USA, the density and arrangement of honey bee hives was either 1.25 acre^{-1} (3 ha^{-1}) in a clumped distribution, 3 acre^{-1} (7.4 ha^{-1}) in a clumped distribution, or 3 acre^{-1} in a dispersed distribution. The number of melons and weight of melons increased as the hive density and degree of dispersal increased. Melon sweetness increased with increasing fruit weight (Eischen and Underwood, 1991).

Artificially delaying bee pollination may stimulate plants to produce more perfect flowers, that is, flowers that can bear fruit. In a 2-year study (Eischen *et al.*, 1994), pollination was delayed for 6 days or 12 days by temporarily netting four varieties ('Cruiser', 'Explorer', 'Mission', and 'Primo') at the onset of female flowering to exclude bees. Hives of honey bees were placed next to the test plot. With

Fig. 27.1. Perfect flower and male flower of cantaloupe, *Cucumis melo*. (Source: Darrell Rainey.)

'Primo' in 1992, delaying pollination by 6 days increased the number of marketable melons (unblemished, > size 30) compared to non-netted control plants or plants netted for 12 days. With 'Mission' in 1993, delaying pollination by 12 days increased the number of fruits per plant (≥ size 23) and total fruit weight compared to controls or plants netted for 6 days. Delaying pollination was generally not beneficial with the other varieties. The greatest advantage of delaying pollination may be that it gives the grower more time to apply insecticides. More controlled pollination episodes may also free beekeepers to use their bees elsewhere until the scheduled days when plant netting is removed.

Row covers are used in some areas to raise air temperatures and speed fruit ripening. However, row covers can exclude pollinating insects. Row covers are usually removed in British Columbia at the first flush of perfect flowers, but it would be desirable to keep the covers on longer in order to continue hastening the ripening process. Fortunately, honey bee hives can be placed under row covers and the bees pollinate cantaloupe under these conditions. Introducing a honey bee colony under a row cover and extending the covered period an extra month hastened ripening, increased yield, and increased fruit weight of cantaloupe in British Columbia (Gaye *et al.*, 1991). A similar concept is used in Israel in the form of long, walk-through tunnels orientated in a north–south direction to enable the structures to withstand strong southern winds. Honey bee hives pollinate optimally under these conditions when they are placed at the north end of the tunnel (Dag and Eisikowitch, 1995). Row covers of spunbonded fabric were used in Senegal to protect cantaloupe plants from numerous pest

Table 27.1. Recommended bee densities for cantaloupe.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
0.5–5 (1.2–12.4)	McGregor (1976)
2–3 (5–7.4)	Atkins *et al.* (1979)
0.1, 0.2, 1.2, 3 (0.3, 0.5, 3, 7.5)	Crane and Walker (1984)
1–2 (2.5–5)	Levin (1986)
1.3, 3 (3.2, 7.4)	Eischen and Underwood (1991)
0.2–3 (0.5–7.5)	Williams (1994)
1 (2.5)	Scott-Dupree *et al.* (1995)
1.8 (4.4)	**Literature average**
Other measures and bees	
1 honey bee per 10 perfect flowers	McGregor (1976)
3 bumble bee colonies per 1000 glasshouse plants	Fisher and Pomeroy (1989)

insects. Yield of export-grade fruit was highest when plants were kept under closed tunnels that were fitted with honey bee hives modified to provide bee entrances to both the inside and outside of the tunnels (Vaissière and Froissart, 1996).

Africanized honey bees foraging on cantaloupe in Costa Rica work more closely to their nests than do European or European × Africanized hybrid bees (Danka *et al.*, 1993a). Thus, Africanized bee colonies used for pollinating cantaloupe should be distributed uniformly throughout a field to ensure adequate pollination by these bees.

Bumble bees effectively pollinate cantaloupe grown in glasshouses in New Zealand (Fisher and Pomeroy, 1989). Bumble bee workers visited cantaloupe flowers from dawn to dusk, and relatively few (~20%) exited through glasshouse windows in order to forage on non-crop plants. With bumble bee pollination, 90% of the crop reached marketable weight.

Chapter 28

Carrot Seed

Flowering

Carrot (*Daucus carota*) is a biennial or winter annual plant, which means it must go through a period of cold to produce flowers and seed.

The umbrella-shaped inflorescences are borne in large groups called umbels. The primary, or king, umbel appears first near the top of the plant, followed by many second-, third-, and fourth-order umbels. Because of this developmental pattern, the plants have flowers and seed at various stages of maturity for 6–8 weeks during summer. Plants will flower for about 1 month, and flowering within a single umbel lasts about 7 days.

The individual white floret is perfect with five stamens and two styles which lead to two compartments in the ovary, each with one ovule; thus, each flower can produce two seeds. Apparently, each floret needs only two grains of pollen to fertilize the two ovules. Anthers release pollen within a floret over 1–2 days, and the stigma becomes receptive on the third or fourth day and stays receptive for a week or more. Nectar is secreted from the upper surface of the ovary. Many types of insects visit carrot for pollen and nectar.

Carrot Pollination Requirements

Most seed set occurs with pollen transferred by insects from different plants, although a small percentage of carrot plants can set seed with their own pollen. Abundant numbers of insect pollinators increase seed yield and hasten its maturity (McGregor, 1976; Free, 1993). Yields of open-pollinated carrot seed in North America are about 850 lb acre^{-1} (952 kg ha^{-1}), and yields for hybrid seed are about 250 lb acre^{-1} (280 kg ha^{-1}).

Table 28.1. Recommended bee densities for carrot.

No. of honey bee hives per acre^{-1} (ha^{-1})	Reference
Open-pollinated	
2 (5)	Mayer and Lunden (1983)
3–4 (7.4–10)	Levin (1986)
3 (7.5)	**Literature average**
Hybrid production	
4–6 (10–14.8)	Mayer and Lunden (1983)
Other measures	
8 honey bees yd^{-2} (9.6 m^{-2})	Hawthorn *et al.* (1960)
6–8 honey bees yd^{-2} (7.2–9.6 m^{-2})	Mayer and Lunden (1983)
7.3 yd^{-2} (8.8 m^{-2})	**Literature average**

Hybrid carrots are valued for their uniform, smooth, and colourful roots. Hybrid seed production requires the transfer of pollen from pollen-donor lines to the stigmas of selected male-sterile lines. Because cross-pollination is so common, stocks are maintained by cooperating breeders who agree to isolate fields of the same stocks far from fields of different stocks.

Carrot Pollinators

Commercial carrot seed production requires insect pollination. Many types of insects visit carrot flowers; however, there are not always sufficient numbers of pollinators. Wild bees and honey bees are the most important pollinators. Of these, only honey bees can be practically managed on a large scale. Hives should be placed in several areas around the field because honey bees tend to work close to their hive.

Honey bees work some varieties more readily than others which can cause large differences in seed set (Erickson and Peterson, 1979a,b). In hybrid seed production, honey bees prefer the pollen-yielding male-fertile plants over the male-sterile (female) plants. A nectar-favouring pollinator that freely visits both types would be preferable in these cases.

Honey bees effectively pollinate carrot, but they do not especially prefer carrot flowers. They are easily lured to more attractive flowering plants.

Chapter 29

Cherry (Sweet, Sour)

Flowering

Sweet cherry (*Prunus avium*) and sour cherry (*P. cerasus*) flowers are white and occur in clusters of 2–5 on short lateral spurs. Each flower is about 1 in (2.54 cm) in diameter, has five petals, one upright pistil with an ovary and two ovules, and about 30 stamens (Fig. 29.1). The flower opens for 3–5 days. The stigma is receptive before the anthers release pollen, but anthers open shortly thereafter. Nectar is secreted near the base of the pistil. Honey bees generally prefer sweet cherry blossoms over sour cherries because sweet cherry nectar is richer; pollen of either type is equally attractive to honey bees.

Cherry Pollination Requirements

Ovules of some cherry flowers begin to degenerate even before the flower opens; therefore, it is important that pollination occurs as soon as possible after the flower opens. The first 20% of flowers that open, if pollinated, will set higher quality fruit than the remaining 80% (Mayer *et al.*, 1988b).

Almost all sweet cherry varieties require cross-pollination with pollen from a suitable pollenizer cultivar (Table 29.1). Main varieties and pollenizer varieties should be interplanted in orchards in order to encourage good cross-pollination. Pollinators, mainly honey bees, must be present in sufficient numbers to transfer pollen from pollenizer to main varieties. The variety 'Stella' is self-compatible and does not require a pollenizer, but it still requires pollinators to transfer pollen from anthers to stigmas.

Problems with poor pollination are well demonstrated with the sweet cherry variety 'Bing'. The 'Bing' stigma needs about 100 grains of pollen from a pollenizer in order to set a good fruit (Mayer *et al.*,

Fig. 29.1. Flower of cherry, *Prunus* species. (Source: Darrell Rainey.)

Table 29.1. Sweet cherry varieties and suitable pollenizers. Blank boxes indicate suitable pollenizer combinations. A '0' indicates varieties that are not suitable pollenizers for each other. An 'X' indicates that the variety is partially self-fruitful but should not be planted in solid blocks.

		Variety pollinated													
		Chelan	Black Tartarian	Royal Ann	Rainier	Van	Bing	Hardy Giant	Black Republican	Stella	Hedelfingen	Royalton	Lambert	Lapins	Gold	Sweetheart
Pollen source variety	Chelan	0														
	Black Tartarian		0													
	Royal Ann			0			0						0			
	Rainier				0											
	Van					0										
	Bing			0			0						0			
	Hardy Giant							0								
	Black Republican								0							
	Stella									X						
	Hedelfingen										0					
	Royalton											0				
	Lambert			0			0						0			
	Lapins															
	Gold														0	
	Sweetheart															

1988b). It takes several bee visits to the same flower to accomplish this. If 'Bing' pollen lands on a 'Bing' stigma, the pollen germinates and grows a pollen tube down to the ovary. This stimulates the fruit to grow for about five weeks, but then the fruit aborts. If too much 'Bing' pollen is growing on a 'Bing' stigma, there is no room for pollen from a pollenizer. In orchards with an inadequate density of pollenizers, much of the pollen on 'Bing' stigmas is 'Bing' pollen. Many cherries will grow to the size of a large pea and then drop.

All of the important sour cherry varieties can set fruit with their own pollen, but only after it is transferred by bees from the anthers to the stigma. However, even sour varieties set more fruit if more than one variety is interplanted in the orchard.

Cherry Pollinators

Ninety-nine per cent of insect visitors are bees in commercial cherry orchards in the northwestern US. Bee-keepers almost never get surplus cherry honey even though honey bees readily work the crop. Cherry nectar is rich in sugar (30–45%); however, 70–95% of honey bee foragers collect pollen (Mayer *et al.*, 1988b).

Table 29.2. Recommended bee densities for cherry.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
Sweet cherry, or general	
1 (2.5)	Schuster (1925); Tufts and Philp (1925); Luce and Morris (1928); Marshall *et al.* (1929)
1–1.2 (2.5–3)	Yakovleva (1975)
5 (12.4)	McGregor (1976)
1–2 (2.5–5)	Levin (1986); Scott-Dupree *et al.* (1995)
1.5–2.5 (3.7–6.2)	Kevan (1988)
2 (5)	Mayer *et al.* (1988b)
1.2 (3)	British Columbia Ministry of Agriculture, Fisheries, and Food (1994)
0.5–1.2 (1.3–3)	Williams (1994)
1.7 (4.2)	**Literature average**
Sour cherry	
0	Kevan (1988)
1–2 (2.5–5)	Scott-Dupree *et al.* (1995)
1 (2.5)	**Literature average**
Other measure	
25–35 honey bees per tree min^{-1}	Mayer *et al.* (1988b)

Wind does not pollinate cherry. Honey bees are the principal pollinators. With either sweet or sour cherries, it is important that pollination occurs as soon as possible after anthers begin releasing pollen. Honey bee hives should be placed in the orchard in groups of 4–12 and no further apart than 100 yards (91.4 m). With sweet cherry, hives should be moved into the orchard on the day bloom begins or one day earlier. With sour cherry, it is better to move hives into the orchard at least one day after bloom begins because sour cherry nectar is less attractive to bees and a higher degree of orchard bloom is necessary to keep honey bees from leaving the orchard and seeking richer forages.

Honey bee attractants have had a mixed record in cherry. The attractant Bee-Scent® increased honey bee visitation for 24 h post-treatment and increased fruit-set by 12% in 'Van' (Mayer *et al.*, 1989a). Bee-Scent Plus® increased fruit-set by 15%. However, an experimental queen mandibular pheromone attractant did not increase bee visits, fruit-set, or fruit size in 'Bing' sweet cherry (Naumann *et al.*, 1994b).

Reproduction of spring-introduced orchard mason bees (*O. cornifrons* and *O. lignaria propinqua*) ranged from 10 to 50% in south central Washington, USA, but these bees were rarely seen visiting cherry flowers (D.F. Mayer, unpublished data). Orchard mason bees may be potential pollinators for commercial cherry in Washington, but more research is necessary to appraise their efficacy.

Chapter 30

Clover Seed (Alsike)

Flowering

Flowers of alsike clover (*Trifolium hybridum*) occur as a head made up of many pink or white florets. Each floret has a large dorsal petal, two lateral wing petals, and two lower keel petals. There are ten stamens; one of them is free and the other nine unite to form a tube that encloses the long ovary (Fig. 30.1). When pressure is applied, as from an insect, the flower trips to expose the stigma. The flower returns to its original position after the pressure is removed, unlike lucerne which remains in the tripped position. Each alsike clover floret produces 2–3 seeds, and in a good year each flower head will produce ~100 seeds. Alsike clover produces plentiful nectar and pollen and many bees visit its flowers.

Alsike Clover Pollination Requirements

Alsike clover is largely self-sterile. This means that individual florets must receive pollen from another plant in order to produce seed. Cage studies consistently demonstrate the value of bee pollination to alsike clover seed yield (Table 30.1). Differences in seed yield per head can translate into large differences in per-acre yields. For example, for a field with 1000 heads yd^{-2} (1200 m^{-2}), 50 seeds per head translates into 350 lb $acre^{-1}$ (392 kg ha^{-1}); 90 seeds per head give 625 lb $acre^{-1}$ (700 kg ha^{-1}); and 120 seeds per head give 825 lb $acre^{-1}$ (924 kg ha^{-1}) (Dunham, 1939). Although the average US yield is ~140 lb $acre^{-1}$ (157 kg ha^{-1}), yields of up to 1000 lb $acre^{-1}$ (1120 kg ha^{-1}) are sometimes reported (McGregor, 1976). This suggests that suboptimal pollination may be limiting yield in alsike clover seed production in the US.

Table 30.1. Benefits of bee pollination to seed yield in alsike clover. Data are numbers of seeds per head in various pollination treatments.

Plants caged with honey bees	Plants caged without bees	Not caged	Reference
122	2	39	Dunham (1939)
107	0.4	57	Crum (1941)
NA	0.4	126	Scullen (1956)
115	**0.9**	**74**	**Averages**

NA, not available.

Alsike Clover Pollinators

Worldwide, honey bees are the most abundant and effective pollinator of alsike clover, although many types of bees visit it (Free, 1993). The floret of alsike clover is readily accessible to honey bees, unlike the more tubular corolla of red clover. Production of nectar and pollen is good, so honey bees are not likely to leave alsike clover in preference for another blooming plant. Honey bees are relatively efficient pollinators of alsike clover. Seed yield in Canada was 375 lb acre^{-1} (420 kg ha^{-1}) with honey bees, but when honey bees were absent and experimenters relied on non-managed bees the yield dropped to 29–293 lb acre^{-1} (32–328 kg ha^{-1}) depending on the numbers of non-managed bees (Pankiw and Elliot, 1959).

Managed leafcutting bees are categorized as 'very good' pollinators of 'Dawn' variety Canadian alsike clover (Richards, 1991).

Table 30.2. Recommended bee densities for alsike clover.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
1–3 (2.5–7.4)	McGregor (1976); Scott-Dupree *et al.* (1995)
1.2–1.6 (3–4)	Háslbachová *et al.* (1980)
1–2 (2.5–5)	Levin (1986)
2–3.2 (5–8)	Kevan (1988)
1–3.2 (2.5–8)	Williams (1994)
2 (4.8)	**Literature average**
Other measures and bees	
3000 honey bees acre^{-1} (7410 ha^{-1})	Dunham (1957)
3240–5260 honey bees acre^{-1} (8000–13,000 ha^{-1})	Háslbachová *et al.* (1980)
20,000 leafcutting bees acre^{-1} (50,000 ha^{-1})	Scott-Dupree *et al.* (1995)

(a)

(b)

Fig. 30.1. (*and opposite*) Inflorescence of a representative *Trifolium* species clover (a). Individual floret of a *Trifolium* inflorescence (b). (Source: (art) Darrell Rainey; (photo) Jim Strawser.)

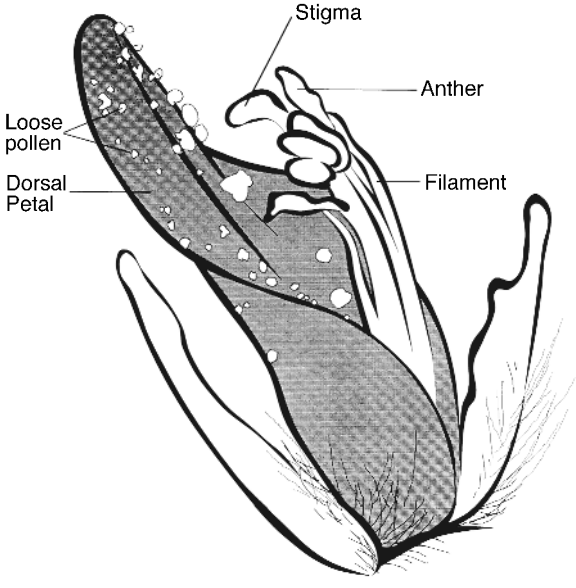


Fig. 30.1. *Continued.*

Chapter 31

Clover Seed (Crimson)

Flowering

The morphology of crimson clover (*Trifolium incarnatum*) flowers is typical of other *Trifolium* species (Fig. 30.1). There are 65–125 reddish florets per head. The crimson clover floret is not as easily probed by honey bees as alsike clover. Nevertheless, honey bees visit crimson clover for nectar and pollen and sometimes make surplus crops of honey. The flower is tripped whenever a bee visits it for nectar or pollen. Once a floret is pollinated it withers within one day. Thus, a well-pollinated field takes on a dull appearance whereas a poorly-pollinated field stays colourful and fresh-looking for up to two weeks.

Crimson Clover Pollination Requirements

Crimson clover is mostly self-fruitful; however, the floret is not self-tripping. Therefore, insect pollination is necessary for achieving acceptable yields (Table 31.1).

Crimson Clover Pollinators

Honey bees are historically the most important pollinator of crimson clover. Compared to yield from plants caged to exclude bees, honey bee pollination increases seed weight per head 2.4 times, number of seeds per head 14 times, and pounds of seed per acre 4–21 times (McGregor, 1976). The number of pods with seeds and seed yields are usually highest near apiaries.

The crop's appearance is a useful indicator of whether pollinator numbers are adequate because the florets wither after they are polli-

Table 31.1. Benefits of bee pollination to seed yield in crimson clover. Data are pounds of seed per acre (kg ha^{-1}).

Plants caged with honey bees	Plants caged without bees	Not caged	Reference
47 (53)	2.7 (3)	57 (64)	Killinger and Haynie (1951)
233 (261)	59 (66)	297 (333)	Weaver and Ford (1953)
NA	41 (46)	212 (238)	Johnson and Nettles (1953)
NA	90 (101)	470 (527)	Beckham and Girardeau (1954)
NA	89 (100)	587 (658)	Blake (1958)
NA	42 (47)	164 (184)	Girardeau (1958)
140 (157)	**54 (61)**	**298 (334)**	**Averages**

NA, not available.

Table 31.2. Recommended bee densities for crimson clover.

No. of honey bee hives $acre^{-1}$ (ha^{-1})	Reference
1–5 (2.5–12.4)	McGregor (1976)
1–2 (2.5–5)	Levin (1986)
2.3 (5.6)	**Literature average**
Other measure	
2–3 honey bees per 100 flower heads	Knight and Green (1957)

nated. When pollinator activity is good, each head has a whorl of open florets with buds above and withered florets below (Weaver and Ford, 1953).

Chapter 32

Clover Seed (Red)

Flowering

The basic design of red clover (*Trifolium pratense*) flowers is typical of other *Trifolium* species (Fig. 30.1). Each rose-pink head is made up of 55–275 florets which open over 6–10 days starting from the base and progressing towards the top. Each floret is $\frac{1}{4}$–$\frac{1}{2}$ in (6.4–12.7 mm) long and $\frac{1}{2}$ in (2.1 mm) in diameter. The ovary of each floret has two ovules, but usually only one develops. The sexual column is made up of ten stamens and a slightly-longer stigma that extends to the mouth of the corolla tube; at its base the sexual column is enclosed within the keel petals. When a bee pushes with its head on the keel petals, the stigma and the anthers are tripped and contact the bee.

Red clover has a relatively long corolla (6.4–12.7 mm) which makes it difficult for short-tongued bees, such as honey bees (average tongue length ~6 mm), to reach the nectaries that occur at the base of the sexual column. This may limit bee visitation on red clover in some conditions. The corolla tube of late-season red clover is usually shorter than that of the first flowering.

Red Clover Pollination Requirements

Red clover is largely self-sterile and needs pollen from another plant in order to set acceptable levels of seed. Bees are the most important pollinators. The floret must be pollinated within 2–4 days after it opens in order to ensure fertilization. Large bee populations should be present during the entire flowering period.

The appearance of red clover flower heads can indicate the degree of pollination accomplished. Pollinated florets soon wither, but if they are not pollinated they stay colourful and fresh-looking. Thus, each head has a whorl of fresh florets with buds above and withered florets

below, and the field takes on a rusty-brown appearance when there are adequate numbers of bees.

Red Clover Pollinators

Honey bees and bumble bees are the most important pollinators of red clover. In general, bumble bees are more efficient on a per-bee basis because they work faster and have longer tongues with which they can more easily work red clover flowers. However, populations of wild bumble bees are unpredictable. Honey bees, on the other hand, are manageable, movable in large numbers, and capable of pollinating red clover in spite of their shorter tongues and relative inefficiency.

Red clover is more easily worked by long-tongued bees, such as bumble bees, because of its long corolla. Species of bumble bee vary in tongue length, and they tend to segregate themselves among crops so that longer-tongued species predominate at crops with longer corollae and vice versa (Ranta and Tiainen, 1982; Fairey *et al.*, 1992). For example, in the Peace River region of Alberta and British Columbia, the long-tongued bumble bee *Bombus borealis* (average tongue length, 10.2 mm) is common on red clover (average corolla length, 7.2 mm), whereas shorter-tongued *B. rufocinctus* (tongue, 7.7 mm) and *B. vagans* (tongue, 8.3 mm) are more abundant on lucerne and alsike clover (corollae, 3.9 mm) (Fairey *et al.*, 1992). Tetraploid red clover varieties produce more nectar than diploid varieties, but their corollae are slightly deeper than those of diploid varieties. Thus, long-tongued bumble bees are the most important pollinators for tetraploid red clovers (McGregor, 1976; Free, 1993).

Long-tongued bumble bees are excellent pollinators of red clover, but some short-tongued species (for example, *B. affinis*, *B. lucorum*, *B. terrestris*, and *B. terricola*) are known to chew holes at the bases of florets through which they rob nectar, completely bypassing the stigmas (Free, 1993). Such robbery holes left by robbing bumble bees are then visited by other bees, such as honey bees, who likewise avoid contacting the stigmas.

Cage studies consistently show that honey bees can pollinate red clover (Table 32.1). However, the real issue is whether sufficient numbers of honey bees reliably occur under field conditions. Honey bees may ignore red clover if there are more accessible nectar sources available nearby. However, nectar may well up in red clover corollae high enough for honey bees to reach it during hot, dry conditions, and honey bee visitation increases dramatically at such times. Pollen-foraging honey bees will deliberately collect red clover pollen from the accessible anthers, and in these cases the depth of corollae is a moot point.

Table 32.1. Benefits of honey bee pollination to seed yield in red clover. Data are numbers of seeds per head under various pollination treatments.

Plants caged with honey bees	Plants caged without bees	Not caged	Reference
61.5	NA	67.3	Richmond (1932)
107	0	57	Crum (1941)
56	1	37	Anderson and Wood (1944)
74.8	**0.5**	**53.8**	**Averages**

NA, not available.

Honey bees are the most important pollinator of red clover owing to their manageability and abundance. Although they collect pollen from red clover, getting nectar can be a problem and colonies in large monocultures may decline for lack of nectar. Sometimes this is confused with pesticide kill. Thus, rented honey bee hives may need regular supplemental feed (sugar or maize syrup), and this extra bee-keeper labour should be reflected in the rental fee. For fields 25 acres or less (≤ 10 ha), bee hives can be grouped in one location. For fields that are larger than 25 acres or fields that are very long and narrow, bee hives should be grouped in two or more locations.

Alfalfa leafcutting bees are known to pollinate red clover. Average seed yield of red clover in northern Alberta, Canada increased from 260 lb acre^{-1} (291 kg ha^{-1}) when leafcutting bees were not used to 366 lb acre^{-1} (410 kg ha^{-1}) when they were used. Furthermore, the

Table 32.2. Recommended bee densities for red clover.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
4–10 (10–25)	Beard *et al.* (1948)
1–3 (2.5–7.4)	Hammer (1950)
1–2 (2.5–5)	Thomas (1951); Johansen (1960)
1–4 (2.5–10)	Johansen and Retan (1971)
1.2–6 (3–15)	Crane and Walker (1984)
3–4 (7.4–10)	Levin (1986)
1–3.2 (2.5–8)	Kevan (1988)
1–4 (2.5–10)	Scott-Dupree *et al.* (1995)
3 (7.7)	**Literature average**
Other measures and bees	
1–18 honey bees yd^{-2} (1.2–21.5 m^{-2})	McGregor (1976)
1 bumble bee yd^{-2} (1.2 m^{-2})	
800 long-tongued bumble bees acre^{-1} (2000 ha^{-1})	Macfarlane *et al.* (1991)

bees reproduced on red clover nearly as well as on lucerne (Fairey *et al.*, 1989). Richards (1991) ranked leafcutting bees as 'very good' pollinators of red clover varieties 'Norlac' and 'Ottawa'.

The most important factor in encouraging good pollinator activity is to maintain good bloom conditions. Honey bee activity is optimized in fields that have large numbers of red blooms. Honey bees will fly to other locations when poor irrigation practices allow brown, water-stressed areas to develop in the field.

Chapter 33

Clover Seed (White, 'Ladino')

Flowering

There are three important types of white clover (*Trifolium repens*): large (namely, 'Ladino'), intermediate, and small. The general design of white clover inflorescences is typical of other *Trifolium* species (Fig. 30.1). Each head has 50–250 florets, and the corollae are about 3 mm long which is short enough to enable most bees to reach the nectar. Stigmas extend beyond the anthers in a fully opened floret, a posture which facilitates cross-pollination. Of the six ovules present in the ovary, each floret produces, on average, about $2\frac{1}{2}$ seeds (McGregor, 1976). White clover is the most common legume forage in northern Europe. It produces abundant nectar and pollen, and the intermediate and small types are the most important honey plants in the US.

White Clover Pollination Requirements

White clover is largely self-sterile and requires pollen from another white clover plant in order to set seed. There are also a few inbred lines that are self-fertile (Michaelson-Yeates *et al.*, 1997).

In spite of the self-incompatibility of most white clover, it is typical for stigmas to be dusted with self pollen even before the flower is fully open (Thomas, 1987; Rodet *et al.*, 1998). It is estimated that the stigma is saturated at a pollen deposition rate of about 300 grains, and about 137 of these grains, on average, can be traced to self pollen passively deposited on the stigma, pollen grains which are rarely capable of successfully fertilizing the ovules. A single bee visit can deposit an additional 115 grains (comprised of various proportions of self or outcross pollen) which, together with the initial passively deposited self pollen, still does not achieve saturation level nor provide an optimum proportion of compatible pollen. Thus, multiple bee visits are

Table 33.1. Recommended bee densities for white clover.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
0.1 (0.2)	Palmer-Jones *et al.* (1962)
0.04–2 (0.1–5)	McGregor (1976)
0.8–1.2 (2–3)	Crane and Walker (1984)
1–2 (2.5–5)	Levin (1986)
2–3.2 (5–8)	Kevan (1988)
0.04–3 (0.1–7.5)	Williams (1994)
1–3 (2.5–7.5)	Scott-Dupree *et al.* (1995)
1.5 (3.7)	**Literature average**
'Ladino'	
2 (5)	Scullen (1956)
Other measure	
2 honey bees yd^{-2} (2.4 m^{-2})	Scullen (1956)

required in order to provide the stigma with an improved ratio of compatible outcross pollen. On average, one honey bee visit achieves 60–70% chance of fertilizing the ovules, but multiple visits are necessary to maximize pollen tube growth to over 90% of ovules (Rodet *et al.*, 1998).

Florets stay open for a week or more if they are not pollinated, but seed set is optimized if cross-pollination occurs soon after the flower opens. For example, seed set in florets pollinated on day five of flowering is 60% lower than in florets pollinated on day one (Jakobsen and Martens, 1994). Florets wilt and turn brown within a few hours after they are visited by a bee (Rodet *et al.*, 1998). Thus, under good pollination conditions a head will have fresh, open florets in the middle with unopened buds above and wilted florets below.

White Clover Pollinators

Honey bees are the most important pollinator of white clover. Intermediate and small white clovers are highly attractive to honey bees which easily work the blossoms and effectively pollinate the stigmas as they probe for nectar or pollen. 'Ladino' clover produces comparatively less nectar and is less attractive to honey bees. Thus, 'Ladino' needs a slightly higher bee density in order to compensate for reduced bee visitation (Table 33.1).

Estimated seed yield of white clover (variety 'Haifa') in open-pollinated plots in Victoria, Australia was 360 lb acre^{-1} (403 kg ha^{-1}), but only 12 lb acre^{-1} (13 kg ha^{-1}) in plots caged to exclude bees. Honey bees made up 95% of bee visitors and 88% of all insect visitors.

Native bees (*Lasioglossum* spp.) made up 5% of bee visitors and 4.3% of all insect visitors (Goodman and Williams, 1994).

Wild bees, including orchard mason bees (*Osmia* spp.) and bumble bees, visit white clover in North America, but they are generally inadequate for commercial pollination needs (Bohart, 1960). Richards (1991) ranked managed leafcutting bees as 'very good' pollinators of white clover in Canada.

As for other *Trifolium* clovers, the appearance of the field is the best indicator of adequate pollinator levels. A field with only fresh, unwilted florets is not getting enough pollination and needs more bees.

Chapter 34

Clover Seed (Sweet Clovers)

Flowering

The inflorescences of white (*Melilotus alba*) and yellow (*M. officinalis*) sweet clover are 1–4 in (2.5–10 cm) racemes with up to 100 white or yellow florets, each floret about $\frac{1}{8}$ in (3 mm) long. The corollae are short which means that short- as well as long-tongued bees can reach the nectar. Stamens and the pistil are enclosed in two petals that form a keel. When a bee presses against the keel, the sexual column springs out, touches the bee, and returns to its original position after pressure is released. Sweet clover produces abundant nectar and pollen, and it is a very important honey plant.

Sweet Clover Pollination Requirements

Sweet clovers range from partially self-fertile to self-sterile. Biennial varieties of either white or yellow sweet clover are more self-sterile than annual varieties (Sano, 1977). The rate of selfing increases in plants in which the pistil and stamens are the same length, and even self-fertile varieties may require bee visitation to trip flowers. Seed yield of most sweet clovers, white or yellow, increases with bee cross-pollination.

Sweet Clover Pollinators

Many types of bees visit sweet clover, but honey bees are by far the most numerous and important. Their benefit to sweet clover seed yield is seen in Table 34.1. Richards (1991) ranked leafcutting bees as 'very good' pollinators of Canadian white sweet clover and yellow sweet clover.

Table 34.1. Benefits of bee pollination to seed yield in sweet clovers. Data are pounds seed produced acre^{-1} (kg ha^{-1}) in various pollination treatments.

Plants caged with honey bees	Plants caged without bees	Not caged	Reference
	Biennial white		
116 (130)	33 (37)	146 (164)	Alex *et al.* (1952)
NA	11 (12)	288 (323)	Holdaway *et al.* (1957)
	Annual white		
157 (176)	16 (18)	130 (146)	Weaver *et al.* (1953)
	Biennial yellow		
248 (278)	130 (146)	396 (444)	Alex *et al.* (1952)

NA, not available.

Table 34.2. Recommended bee densities for sweet clover.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
1–10 (2.5–25)	McGregor (1976)
1–2 (2.5–5)	Levin (1986)
2–3.2 (5–8)	Kevan (1988)
1–3 (2.5–7.4)	Scott-Dupree *et al.* (1995)
3 (7.2)	**Literature average**

Chapter 35

Cotton

Flowering

There are two important species of cotton grown in North America – upland or short staple cotton (*Gossypium hirsutum*) and long staple or 'Pima' (*G. barbadense*). The cotton flower is 2–4 in (5–10 cm) long and 2 in (5 cm) wide. It has five petals and a staminal sheath with numerous stamens surrounding a style which leads to an ovary at the flower's base (Fig. 35.1). The ovary has 3–5 compartments, each with 5–10 ovules or potential seeds. The flower opens for only one day, and the corolla and staminal column fall off on the second day. The stigma is relatively accessible to cross-pollination in 'Pima', but in upland cotton the stigma is more closely surrounded by the anthers which makes cross-pollination more difficult. Nectar is secreted in the flower and in extrafloral nectaries on the foliage. The crop is sometimes attractive to bees, and they may make surplus cotton honey if insecticide pressure is low. At other times, honey bees avoid cotton flowers even when nectar is abundant. This may be explained by cotton nectar's relatively low sucrose content (sucrose is very attractive to honey bees). Nectar secretion is higher in 'Pima' cotton than in upland cotton (McGregor, 1976).

Cotton Pollination Requirements

Cotton is mostly self-pollinating and self-fertile. However, bee pollination increases seed set per boll and cotton yield in 'Pima S-1' and earliness of seed set in upland 'A-33' and 'A-44' (McGregor, 1976). Bee pollination often increases boll set, seeds per boll, seed weight, cotton per boll, boll weight, total cotton yield, uniformity of boll ripening, and decreases shedding of bolls (McGregor, 1976; Free, 1993). Stigmas of bagged flowers are not always completely covered with pollen, but

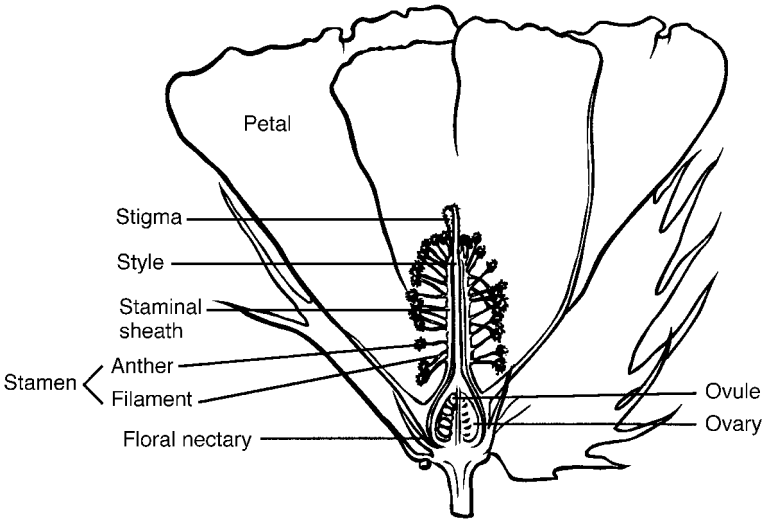


Fig. 35.1. Flower of cotton, *Gossypium* species. (Source: Darrell Rainey.)

this is rarely the case with open flowers when insect visitation is high (Kearney, 1923). Thus, the measurable benefits from bee activity probably derive from bees increasing the amount and distribution of pollen on stigmas. The stigma needs about 100 viable pollen grains in order to set a boll (Waller and Mamood, 1991).

Benefits may also derive from bee-mediated cross-pollination, but this is not universal. Pollen tube germination and growth rate in 'Pima' can be either faster or slower with foreign pollen (Kearney, 1923). Uncontrolled cross-pollination is undesirable in breeding programmes because it introduces off-type progeny.

Historically, cotton is one of the most insecticide-intense cropping systems in the US, and it sets acceptable yields under conditions which discourage the presence of bees. However, reduced pest pressures and insecticide inputs may free cotton growers to take advantage of the yield-enhancing benefits of bee pollination. The boll weevil eradication programme has virtually eliminated the cotton boll weevil from large areas of North Carolina, South Carolina, Georgia, and Florida (Haney and Lewis, unpublished report). Insecticide applications have dropped as a result and bee-keepers now report crops of surplus cotton honey – something unthinkable only a few years ago. Thus, using bees commercially for cotton pollination is not far-fetched, but research is needed to see if this practice is profitable for cotton growers and bee-keepers.

Hybrid cotton seed production

When different varieties of cotton are crossed, the resulting progeny sometimes performs better than either parent line. This is common in plant and animal agriculture and is called *hybrid vigour*. Production of hybrid cotton seed was made possible with the development of male-sterile lines that cannot produce viable pollen (Meyer, 1969). Because male-sterile lines cannot pollinate themselves, controlled crossing is possible when a selected male-fertile line is grown nearby and pollinators are present. Honey bee hives are rented for this purpose in Texas and the southwestern US. Yield of hybrid seed is highest when four rows of male-sterile cotton are alternated with two rows of male-fertile (Loper, 1987). The transfer of pollen grains to stigmas and the seed yields per boll are higher in male-sterile rows grown immediately next to male-fertile rows, but if honey bee populations are large enough every pistil is pollinated regardless of its location (DeGrandi-Hoffman and Morales, 1989).

Honey bees sometimes prefer one parent line over the other, in which case the rate of crossing is reduced. Honey bees prefer the male-sterile line more often (Waller *et al.*, 1985a), but sometimes they show no preference (DeGrandi-Hoffman and Morales, 1989). It is ideal if the grower can interplant lines that have similar flower colour, morphology, and nectar characteristics. Barrier rows of male-sterile lines (Loper, 1987) or isolation may be necessary to protect the parental male-sterile line from unwanted crossing.

Cotton Pollinators

Many types of insects visit cotton, but in North America the most important pollinators are honey bees, bumble bees, and certain species of carpenter bees.

Almost all honey bee visits to cotton flowers are for nectar, but bees inevitably get pollen on their bodies as they probe the flower. Little cotton pollen is transferred to nestmates in the hive (Loper and DeGrandi-Hoffman, 1994), so pollination is most likely with bees that visit two or more flowers in succession. Honey bees often prefer the extrafloral nectaries, and such plant visitors are useless as pollinators. If this behaviour becomes a problem, the best solution is to increase hive densities in order to saturate the field with pollinators. Honey bees are the most important pollinator of cotton worldwide in spite of their preference for extrafloral nectaries (Table 35.1).

Cotton pollen is well suited to insect transport, but it is not equally attractive to all bees. The pollen's spiny shape makes it difficult for honey bees to pack it in their pollen baskets. Thus, honey bees rarely

Table 35.1. Effects of honey bees on yield in cotton.

Effects of honey bees	Reference
Increased yield 24.5% in 'Pima S-1'	McGregor *et al.* (1955)
Increased yield 22.4% in 'Ashmouni'	Wafa and Ibrahim (1960)
Increased boll set 12%, seeds per boll 5%, and seed cotton (seed + lint) per boll 11%	Moffett *et al.* (1978)
Increased bolls m^{-1} 37.6% and seed cotton m^{-1} 29.9% in normal male-fertile line	Waller *et al.* (1985b)

collect cotton pollen deliberately although they pick up pollen as they visit flowers for nectar (Vaissière and Vinson, 1994). This is apparently not the case with bumble bees which readily collect cotton pollen in the field. Bumble bees have more cotton pollen on their bodies compared to honey bees, and the number of seeds per boll is higher in male-sterile plants caged with bumble bees than in plants caged with honey bees (Berger *et al.*, 1988).

In cage tests, carpenter bees (*Xylocopa varipuncta*) increased bolls per metre, bolls per plant, seed cotton (seed + lint) per metre, seed cotton per plant, and seed cotton per boll in a male-sterile hybrid parent line. However, the bees did not affect yield in a normal male-fertile line (Waller *et al.*, 1985b).

Table 35.2. Recommended bee densities for cotton.

No. of honey bee hives $acre^{-1}$ (ha^{-1})	Reference
0.2–5 (0.5–12.4)	McGregor (1976)
1–2 (2.5–5)	Levin (1986)
2 (5)	**Literature average**
Other measure	
10 honey bees per 100 flowers	McGregor (1959)

Chapter 36

Cranberry

Flowering

Cranberry (*Vaccinium macrocarpon*) is native to North America. The flower is $\frac{1}{4}$–$\frac{1}{3}$ in (0.6–0.8 cm) long and contains 5–8 stamens tightly compacted to form a tube surrounding a single style (Fig. 36.1). The flower hangs downward, and when it opens the four petals bend back to fully expose the sexual column. For the first 2 days the anthers release pollen while the stigma remains dry, unreceptive, and hidden inside the ring of stamens. But the style keeps growing and by the time the flower has shed its pollen the stigma has become exposed, sticky, and receptive. Thus, the flower's behaviour discourages selfing. There are nectaries at the base of the flower and bees probing for nectar at young flowers are dusted with pollen. Cross-pollination occurs when bees visit older flowers that have receptive stigmas. The pollen is heavy and not wind-borne, thus bees are the primary pollinator. Each pollen grain can generate up to four pollen tubes, and each ovary has 24–36 ovules; thus, it takes only a few pollen grains to set a fruit. Petals of newly opened flowers are white or slightly pink. Petals may stay attached for up to three weeks and change to a rosy pink if the flower is not pollinated. A rosy hue to a field indicates inadequate pollination.

For bees, cranberry is a marginal source of pollen and a poor source of nectar. Yet nectar is crucial to the pollination process and without it bees would not visit the older flowers that have atrophied anthers and receptive stigmas. The variety 'Stevens' in New Jersey produces 25–35% more nectar sugar per flower than either 'Ben Lear' or 'Early Black', and the nectar secretion rate of 'Stevens' was not improved by a two-year fertilization programme (Cane and Schiffhauer, 1997). This study suggests that nectar production is at least partly under genetic control and, therefore, a viable character for cranberry breeding programmes.

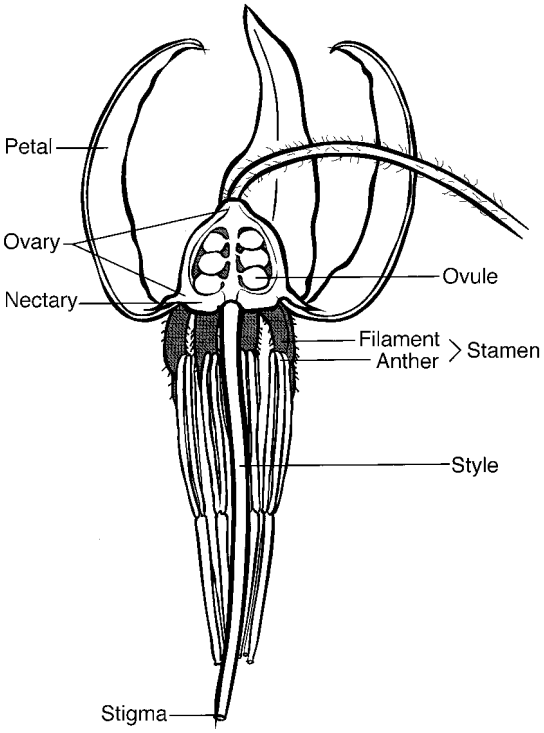


Fig. 36.1. Flower of cranberry, *Vaccinium macrocarpon*. (Source: Darrell Rainey.)

Cranberry Pollination Requirements

Because pollen release and stigma receptivity are separated in time, insects are necessary in order to move pollen from active anthers to receptive stigmas in different flowers. Wind is not an important pollinator of cranberry. Cranberry typically sets no more than 40–50% of its flowers (Marucci and Moulter, 1977). Although the authors attribute this to 'natural attrition or overproduction of blossoms', they also say that high bee concentrations help plants attain their maximum potential fruit-set. Thus, insect pollination may be a limiting factor in cranberry production and growers should encourage large bee numbers to ensure maximum yields.

Cranberry may benefit from cross-pollination among varieties. Fruit-set is relatively high (~73%) in New Jersey, USA, bogs in which vines of different varieties grow alongside each other, and cross-pollination increased fruit-set, seed number, and fruit size in more controlled tests (Marucci and Moulter, 1977).

Cranberry Pollinators

Many species of bees visit cranberry, but few occur in large numbers. The diversity of bee species is high in cranberry in southeastern Massachusetts, USA, but only honey bees and bumble bees (mainly *B. impatiens* and *B. bimaculatus*) occur in large numbers (MacKenzie and Averill, 1995). Bumble bees are numerous in abandoned and natural bogs, whereas honey bees are numerous only in cultivated bogs in which bee hives are imported. Native solitary bees are more abundant and species-rich in abandoned and natural bogs than in cultivated areas – a trend also found by MacKenzie and Winston (1984) in British Columbia, Canada.

Honey bees and the bumble bees *B. mixtus, B. occidentalis,* and *B. sitkensis* are the most numerous cranberry pollinators in Washington, USA (Patten *et al.*, 1993). Honey bee visitation on cranberry peaks at 3 p.m., whereas bumble bees are more constant throughout the day.

About 25 species of insects visit cranberry in cultivated bogs in Ontario, Canada (Kevan *et al.*, 1983). The bumble bees *B. terricola* and *B. vagans* are abundant and avidly work cranberry flowers.

The native solitary leafcutting bee *Megachile addenda* has shown promise as a cranberry pollinator in southern New Jersey (Cane *et al.*, 1996). The females forage for cranberry pollen with which they provision their subterranean nests, and they are efficient pollinators. The daily foraging activity of one female may account for 1291–1440 berries. Commercial management of these bees, however, is limited by high rates of nest parasitization.

Honey bees are not efficient pollinators of cranberry. Bumble bees work the flowers more rapidly and their pollen loads are less contaminated with pollen from other plant species. Bumble bees rarely rob flowers, that is, probe for nectar from the flower base while avoiding contact with the stigma (MacKenzie, 1994). In cultivated bogs in Ontario with imported honey bee hives, the number of honey bees foraging on cranberry was low regardless of the distance from the hives, and few honey bees were foraging on cranberry farther than 220 ft (200 m) from the hives (Kevan *et al.*, 1983). Consequently, fruit yield and number of seeds per flower were unaffected by distance from honey bee hives. Honey bees were attracted to numerous competing nectar sources, and the authors suggest that honey bees may be more effective in very large bogs where densities of native bees and competing nectar sources are comparatively low.

Because bumble bees are good pollinators and occur naturally near bogs, cranberry production and bumble bee conservation are, conceptually at least, a perfect match. There are three ways to go about this – to leave idle land undisturbed for bumble bee nesting sites; to grow supplemental bee pasture plants in field margins; and to

Table 36.1. Recommended bee densities for cranberry.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
0.2–10 (0.5–25)	McGregor (1976)
3–4 (7.4–10)	Levin (1986)
1 (2.5)	Kevan (1988)
2 (5)	Macfarlane *et al.* (1994)
1 (2.5)	Scott-Dupree *et al.* (1995)
3 (7.6)	**Literature average**
Other bees	
443 bumble bees acre^{-1} (1100 ha^{-1})	Hutson (1925)
451 *Megachile addenda* females acre^{-1} (1114 ha^{-1})	Cane *et al.* (1996)

provide artificial nest boxes along bog edges (see Chapter 8, pages 67 and 69). Supplemental bee pastures made up of borage (*Borago officinalis*), bee plant (*Phacelia tanacetifolia*), catmint (*Nepeta mussinii*), and anise hyssop (*Agastache foeniculum*) grown alongside Washington cranberry bogs were attractive to bumble bees, but the long-term benefit of the effort was uncertain (Patten *et al.*, 1993). In general, bumble bee conservation efforts are not measurably successful in Washington cranberry (D.F. Mayer, personal observation).

Honey bees are widely used for commercial cranberry pollination in spite of their relative inefficiency. Honey bee hives are easily moved into bogs, thus raising enormously the number of bees foraging on cranberry (MacKenzie and Averill, 1995). Honey bee densities in Washington at the one hive per acre (2.5 ha^{-1}) rate resulted in 25–43 more barrels of cranberries than did densities at half that rate (D.F. Mayer, unpublished data). Although native bees, especially bumble bees, are good pollinators, they do not always occur in large numbers (MacKenzie and Winston, 1984). Thus, honey bees are the most practical way to ensure cranberry pollination.

Honey bee hives that are established and acclimated to a cranberry bog seem to outperform colonies imported just before the pollination season, unlike the pattern for most other crops. Caucasian honey bees seem to work cranberry better in cool weather than do Italian strains. Bees can set most cranberry flowers in about 4 days of good flight activity. Thus, bee-keepers should leave bee hives on bogs for at least 1 week of good weather. It may take 3 weeks of real time in order to accumulate one week's worth of good weather.

Chapter 37

Cucumber

Flowering

Cucumber (*Cucumis sativus*) is normally monoecious which means that there are both male and female flowers on the same plant (Fig. 37.1). Male flowers occur in clusters with each flower on a slender stem and housing three stamens. Female flowers occur singly and are distinguishable by the large ovary at the flower base. The ovary has three chambers, several rows of ovules, and is connected to a short, thick style with three stigma lobes. Flowers have yellow, wrinkled petals. Both male and female flowers produce nectar, and most bee visitors are collecting nectar. Female flowers produce a higher volume of nectar than male flowers, but sugar concentration is higher in male flowers (Collison, 1973). Bees readily visit cucumber, but it is not a rich source of pollen or nectar and bees quickly switch to more attractive plants growing nearby. Cucumber pollen grains are large and sticky and well suited to pollination by bees rather than wind. The stigma is receptive throughout the day but most receptive in early morning (Seaton *et al.*, 1936).

Male flowers open about 10 days before female flowers and outnumber female flowers at least ten to one in ordinary monoecious varieties. These varieties are planted at a rate of 5000–15,000 plants acre^{-1} (12,350–37,000 ha^{-1}). Harvesting the fruit stimulates the plant to produce more flowers and fruit, so several hand-harvests are possible. If fruit remains unharvested it inhibits the formation of new female flowers and fruit on the same vine.

Gynoecious varieties (with almost exclusively female flowers) were developed in order to provide a rapid succession of female flowers and a highly uniform crop suitable for one destructive, machine harvest. These varieties are grown in dense plantings of about 50,000 to 150,000 plants acre^{-1} (123,500–370,500 ha^{-1}).

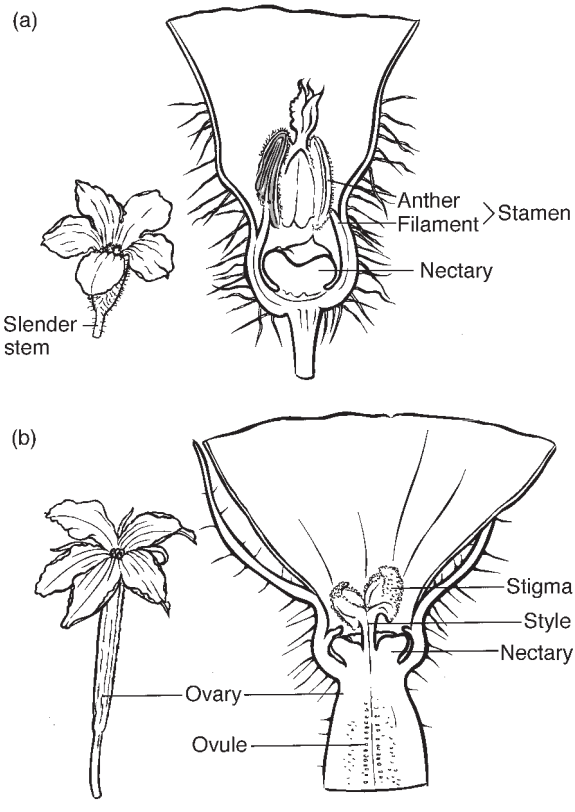


Fig. 37.1. Flower of cucumber, *Cucumis sativus*. (a) male, (b) female. (Source: Darrell Rainey.)

Cucumber Pollination Requirements

Most cucumbers, whether monoecious or gynoecious, require insects to transfer pollen between flowers of the same or different plant. Fruit abortion can reach 100% in flowers bagged to exclude insect visitors (Stanghellini *et al.*, 1997), but self-pollination rates of 30–36% have been documented in the absence of insects (Jenkins, 1942; Gingras *et al.*, 1999), and a small rate of parthenocarpy is known to exist (Gustafson, 1939; Gingras *et al.*, 1999). Nevertheless, insect pollination is the norm.

All of the major varieties are interfertile. Each stigma should receive several hundred grains of pollen for best fruit-set and quality (Seaton *et al.*, 1936). Pollen grains do not necessarily need to be spread evenly on all three lobes of the stigma to form a good fruit, but it does

take multiple bee visits to optimize fruit-set. The minimum number of required bee visits per flower is probably variety-dependent and has been recorded as 8–12 (Connor, 1969; Stephen, 1970; Lord, 1985), ≥ 18 (Stanghellini *et al.*, 1997), and six (Gingras *et al.*, 1999).

About 30% of the flowers in gynoecious plantings should be male in order to optimize pollination and economic return (Connor and Martin, 1971). This means that gynoecious varieties require a supplemental source of male flowers. One way this is done is by pre-mixing commercial seed with around 10% monoecious seed.

Cucumbers produced from early flowers on young plants often have fewer seeds and inferior shape compared to fruit produced without competition on more mature vines (Connor and Martin, 1970). In unpublished studies these authors found that older vines produce larger female flowers with more ovules. Thus, fruit quality may be improved if pollination could be delayed until vines are more mature. Connor and Martin tested this idea with selected monoecious, gynoecious, and gynoecious hybrid varieties. Delaying pollination (with cages to exclude or include bees) for up to 11 days after the first appearance of female flowers increased the number of fruit per plant and the dollar value per acre. The increase was likely due to stronger vine and root growth in more mature plants.

It is difficult to realize the benefits of delayed pollination under field conditions. The only way to delay pollination in monoecious varieties is to delay importation of honey bee hives, but one cannot practically keep wild bees from visiting the plants. With gynoecious varieties, one can interplant male-bearing monoecious pollenizer varieties a few days after planting the gynoecious variety. That way, male flowers become available to bees only after gynoecious plants have reached a suitable level of maturity. Connor and Martin (1969a,b) recommended alternating a 40-ft (12 m)-wide strip of gynoecious variety with a narrow strip of monoecious pollenizer planted a few days after the gynoecious variety. The strip of monoecious pollenizer should probably be no wider than 3 ft (1 m) (Free, 1993). Delayed pollination in gynoecious varieties is further complicated by the fact that even gynoecious plants produce a few male flowers.

In contrast to the results of Connor and Martin (1970), delaying pollination in high-density plantings of the variety 'Napoleon' in Texas did not increase yield (Underwood and Eischen, 1992).

Cucumbers are grown in Europe that set fruit parthenocarpically without pollination. Pollination is undesirable in this context because it results in misshapen, devalued fruit. Growers exclude pollinators with modified glasshouses and government-enforced restrictions on bee-keeping (Free, 1993).

Cucumber Pollinators

Honey bees are the most important pollinator of cucumber, and numerous studies have documented their efficacy (Table 37.1).

Bees collect pollen on cucumber in early morning and switch to nectar later in the morning. Pollen foraging in Maryland, USA is highest before 10 a.m. and decreases dramatically in the afternoon (Tew and Caron, 1988b). Over 80% of honey bee visits in Michigan occur between 9 a.m. and 2 p.m. (Collison, 1976). The stigma is most receptive to pollen in the morning. The first honey bee to visit a flower coats a large portion of the stigma with pollen, and over 40% of flowers receiving one bee visit will set fruit. Although there is less receptive surface on the stigma with each succeeding visit, multiple bee visits per flower (within the range of 1–20) increase fruit-set and average number of seeds per fruit (Collison, 1976).

Large bee populations are especially important in gynoecious plantings where there is an enormous density of female flowers requiring bee visitation.

Cucumber growers are often interested in chemical bee attractants because honey bees are easily distracted away from cucumber to more attractive forages. Unfortunately, the research record for attractants in cucumber is not encouraging. Bee-Scent® attractant in North Carolina cucumber did not increase honey bee visitation, yield, or monetary return (Schultheis *et al.*, 1994).

Bumble bees pollinate field cucumber effectively in North Carolina (Stanghellini *et al.*, 1997). The number of aborted fruit

Table 37.1. Effects of honey bees on yield in cucumber.

Effects of honey bees	Reference
Increased yield in plots caged with bees > 400% compared to plots without bees	Alex (1957a)
Increased yield in plots caged with bees > 160% compared to plots without bees	Canadian Department of Agriculture (1961)
Increased yield 37.5% and 47.5% in two fields with supplemental hives compared to fields without supplemental hives	Kauffeld and Williams (1972)
Increased weight of fruit per plant > 340% in glasshouses with bees compared to glasshouses without bees	Lemasson (1987)
Increased yield per plant almost 3 times higher in plots with bees compared to plots without bees	Gingras *et al.* (1999)

Table 37.2. Recommended bee densities for cucumber.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
1–3 (2.5–7.4)	McGregor (1976)
> 3 for gynoecious hybrids (> 7.4)	
2–3 (5–7.4)	Atkins *et al.* (1979)
≥ 3 for gynoecious hybrids (≥ 7.4)	Hughes *et al.* (1982)
1–2 (2.5–5)	Levin (1986)
0.1–4 (0.3–10)	Williams (1994)
2.2 (5.5)	**Literature average**
Other measures	
1 honey bee per 100 flowers	McGregor (1976)
1 honey bee colony per 50,000 plants	Connor (1969)

decreases as the number of flower visits by either bumble bees or honey bees increases. The rate of abortion is lower with bumble bees when compared at an equal number of bee visits.

Chapter 38

Kiwifruit

Flowering

Kiwifruit (*Actinidia deliciosa*) vines are dioecious which means that vines have either male flowers or female flowers. Male vines produce more flowers than do females. The flowers are $1\frac{1}{2}$–2 in (3.8–5 cm) diameter, have 5–6 white petals, and occur singly or in groups of three (Fig. 38.1). Petals change colour from white to yellow as they age. The female flower has 165–200 stamens that release sterile pollen, up to 41 functioning stigmas, and a swollen ovary containing up to 1500 ovules. The male flower has a non-functioning ovary and 134–182 stamens that release viable pollen (Hopping and Jerram, 1979).

Both male and female flowers release pollen but neither produces nectar. Female vines bloom for 2–6 weeks. Stigmas are receptive as soon as the flower opens and stay receptive for the next 7–10 days (Ford, 1970; Sale, 1983). Receptivity drops sharply after the fourth day, at least in the cultivar 'Hayward' in Spain (González *et al.*, 1995). Female anthers release pollen gradually through a longitudinal split that opens over a 5-day period (Goodwin, 1986a). Male vines bloom for 2–4 weeks and their flowers also release pollen through a longitudinal split, but only for about three days. Male pollen is most abundant in an orchard in morning and early afternoon (Goodwin, 1995). Female pollen is sticky and remains exposed at the split until it is picked up by an insect. Male pollen, on the other hand, is dry and readily falls from the flower when it is shaken.

Kiwifruit Pollination Requirements

Male and female plants must be interplanted in orchards to provide viable male pollen for female stigmas. Male pollenizer cultivars must bloom at the same time as the main female cultivar. In New Zealand

the recommended ratio of male vines to female and their configuration in the orchard are not firmly fixed. Orchards are planted in a configuration of one male to eight female plants with male vines as every third plant in every third row. Other options are to plant in a one male to five female configuration with males as every third plant in every second row or as every second plant in every third row (Free, 1993). Male ratios as high as 1 : 3 have been recommended (Sale, 1984). A comparison of orchards with male densities ranging from 1 : 3 to 1 : 8 showed no differences in average fruit weight or seed number among orchards (Goodwin *et al.*, 1999).

Some growers use overhead male vines which are trained to run at right angles across the tops of female vines (Sale and Lyford, 1990). It is possible to train male vines with wire or wood supports so that they extend into all-female rows; this increases the chance of bees visiting male and female flowers on the same foraging trip. Other growers use strip vines which are narrow rows of male vines trained to run in the same direction as female vines. With either overhead or strip male vines, there is an average 2.3% reduction in fruit seed number with every 1 m increase between male rows (Goodwin *et al.*, 1999). The authors suggested that rows of overhead or strip vines should be planted as close together as possible within the constraints of other considerations such as the total area dedicated to male canopy. It has

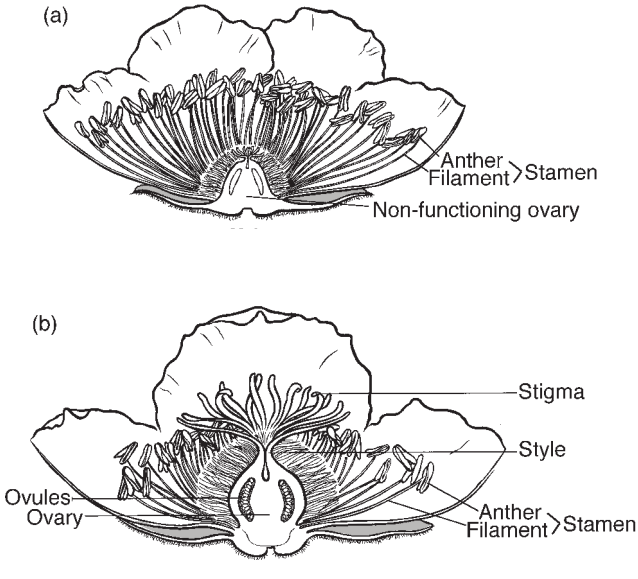


Fig. 38.1. Flower of kiwifruit, *Actinidia deliciosa*. (a) male, (b) female. (Source: Darrell Rainey.)

been suggested that male vines should probably not exceed 10% of the total orchard area (Free, 1993).

Kiwifruit vines do not flower prolifically, and 90% of the flowers must set in order to achieve a commercially acceptable crop (Sale, 1983). The ovary contains many seeds, and there is a positive relationship between fruit weight and the number of seeds set (Hopping, 1976; Pyke and Alspach, 1986). In New Zealand, 700–1400 seeds must set to produce fruit suitable for export (Hopping and Hacking, 1983). Each female pistil needs about 3000 pollen grains to set 700 seeds (Hopping, 1982).

Kiwifruit Pollinators

Wind and honey bees are the most important pollinators of kiwifruit, but their comparative importance is difficult to interpret. Viable male pollen is easily shaken loose from flowers and borne by wind, so kiwi appears well suited to wind pollination. Sterile female pollen is sticky fruit and well suited to insect transport even though it has low nutritive value for bees (Schmid, 1978; Jay and Jay, 1993). Regardless of these characteristic differences, bees visit both male and female flowers to collect pollen. A successful pollinator must be able to carry viable male pollen to female flowers.

Costa *et al.* (1993) compared the relative performance of wind and honey bees in a 2-year experiment in Italy with specially-designed cages that excluded or included insects but did not significantly affect wind speed. During 1 year, vines in wind-only cages set fruit as well as those in bees + wind cages, as well as open-pollinated vines, and as well as hand-pollinated vines. The addition of bees to wind-pollinated cages increased fruit-set one year, yield both years, and average fruit weight one year. In both years, yield and average fruit weight were highest in hand-pollinated vines, but since it takes about 40 man-hours to hand-pollinate 1 acre of kiwifruit (100 hours ha^{-1}) hand-pollination is not considered a practical alternative. Although wind can account for up to 29% of commercial pollination (Clinch and Heath, 1985), honey bees are the most abundant and practical pollinator of kiwifruit (Palmer-Jones and Clinch, 1974; Clinch, 1984).

Honey bees do indeed pollinate kiwifruit. Average fruit weight in New Zealand is increased by 21.4 g and seed number by 227 in flowers that receive one honey bee visit compared to fruit from flowers netted to exclude bees (Donovan and Read, 1991). Fruit-set in France is 5.9% in flowers pollinated by wind only but increases to 39.7% in flowers pollinated by wind + one honey bee visit (Vaissière *et al.*, 1996).

Honey bees often prefer flowers of one sex and return to those flowers on successive trips (Goodwin, 1985; Goodwin and Steven,

1993). Bees doing so presumably transfer little male pollen to female stigmas. This tendency is greatest when bee populations are low (Goodwin, 1986b). Thus, by increasing bee density one can increase competition for pollen, increase bee movement between flowers, and increase the chances for pollination. In spite of their bias for one flower type, about 87% of honey bees foraging on kiwifruit do carry pollen from both sexes, compared to 56% of bumble bees (Macfarlane and Ferguson, 1984). Bees favouring one type of flower can still pick up the opposite pollen from previous flower visitors or by contact with nestmates in the hive.

Honey bees concentrate on the anthers and rarely contact the stigmas uniformly while working a flower. For example, honey bees contact 25% of the stigmas during one flower visit, compared to 48% contact by bumble bee workers and 68% contact by bumble bee queens (Macfarlane and Ferguson, 1984). These data highlight the importance of multiple bee visits in order to achieve satisfactory pollination of a kiwifruit flower. Donovan and Read (1991) estimate that each flower needs about four honey bee visits in order to produce fruit of export size.

Feeding honey bee colonies sugar syrup may improve their efficiency as kiwifruit pollinators. Colonies fed 1 l (~1 qt) of sugar syrup every 1–2 days collect significantly more kiwifruit pollen compared to colonies not receiving syrup. Morning feedings seem to yield the best results, and daily smaller feedings are better than larger, less frequent feedings (Goodwin and Houten, 1991). The effects of feeding syrup do not depend on the type of syrup feeder (top feeder or division board), syrup concentration (1 M or 2 M), or grade of sugar (white or industrial raw); feeding bees dry sugar does not increase kiwifruit pollen collection (Goodwin *et al.*, 1991).

Feeding colonies syrup probably stimulates house bees to process syrup; thus there are fewer of them ready to relieve incoming nectar foragers of their nectar loads. This discourages nectar foragers from collecting more nectar and causes them to shift to collecting pollen which they can pack into cells without help from house bees. This speculation is only partly supported by field data in kiwifruit, but it remains the best explanation for the stimulating effects of syrup. More importantly, it is still uncertain whether increased pollen collection translates into increased kiwifruit pollination and yields.

Honey bee colonies often decline while they are in kiwifruit orchards probably because of competition from high colony densities and the poor nutrient quality of female kiwifruit pollen. Feeding colonies supplemental pollen substitute patties (Herbert and Shimanuki, 1980) while they are in kiwifruit orchards does not affect the amount of kiwifruit pollen they collect nor the amount of honey they produce (Goodwin *et al.*, 1994). In other words, feeding pollen

substitute patties does not impair pollination (and probably improves overall colony condition), but does not increase subsequent honey production.

Large bee populations are important because honey bees are easily distracted away to more attractive crops, and kiwifruit requires a high percentage of fruit-set. The standard recommendation is 3.2 colonies acre^{-1} (8 ha^{-1}) (Palmer-Jones and Clinch, 1974). Even more colonies (> 50% above recommended rate) are needed when flowering is compressed, as is done with hydrogen cyanamide (Goodwin, 1989; Goodwin *et al.*, 1990). Placing hives in groups of 3–4 at the end of each block (1.2–2 acres, 0.5–0.75 ha) of vines disperses foragers evenly throughout the orchard, making it unnecessary to distribute hives singly along rows (Jay and Jay, 1984).

Associations of pollinating bee-keepers in New Zealand use published hive strength standards and contract independent auditors to sample members' hives for compliance. The goal is to ensure that bee-keepers provide colonies of a consistent, acceptable standard for kiwifruit pollination. The following standards are widely used in New Zealand (Matheson, 1991).

Each honey bee colony for pollinating kiwifruit should have the following:

- At least seven full-depth Langstroth frames, each 60% full of brood;
- At least 25% of the brood unsealed;
- Most of the brood in the lower box of the hive;
- A young, prolific queen;
- At least 12 full-depth Langstroth frames covered with bees;
- Sufficient empty combs to encourage colony expansion;
- Enough honey stores to sustain the colony while in the orchard; and
- No American foulbrood disease.

Alfalfa leafcutting bees are not promising pollinators of kiwifruit in New Zealand. In three field sites and one cage test, only four male leafcutting bees were seen on kiwifruit flowers in normal field conditions; pollen retrieved from bees was entirely non-kiwifruit pollen, and kiwifruit petals and leaves were unsuitable for nesting material (Donovan and Read, 1988).

Chapter 39

Onion Seed

Flowering

The onion (*Allium cepa*) inflorescence is an oval umbel 6–8 in (15.2–20.3 cm) across at the top and made up of 50–2000 florets (Fig. 39.1). Each floret is about $\frac{1}{8}$ in (3–4 mm) long and has six stamens divided into two whorls of three each, a style with a three-lobed stigma, and a three-celled ovary with two ovules in each cell. The anthers of the inner whorl open first and release pollen at irregular intervals, followed by those of the outer whorl. The period of pollen release lasts for 24–36 h and is completed before the stigma is receptive. Most of the pollen is released between 9 a.m. and 5 p.m. on the first day the flower is open. There are nectaries at the bases of the inner whorl of stamens. The style continues to grow while pollen is being shed. After all the pollen is released, the style reaches its maximum length and the stigma becomes receptive. Thus, the behaviour of individual florets discourages selfing, but because an umbel contains many florets at different stages of development it is possible for plant selfing to occur. The stigma remains receptive for up to 6 days, but the ability of pollen to germinate on its surface declines after the first day. Pollen is more viable in the morning than in the afternoon. Only a few florets on an umbel will open at the start of flowering. However, the number increases gradually until full bloom when there may be 50 or more open florets. A field of onion can be in various stages of bloom for over 30 days.

Onion Pollination Requirements

An individual floret cannot pollinate itself. Pollen must come from a different floret on the same or different umbel. Onion is partly self-compatible, but cross-pollination between plants is common in open-pollinated plots.

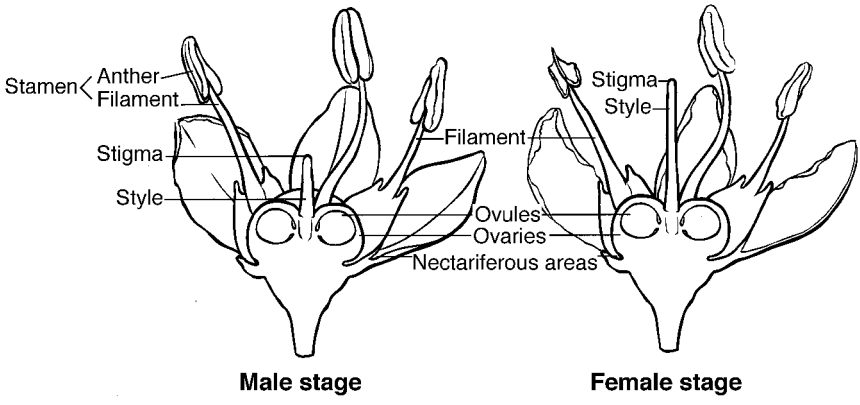


Fig. 39.1. Flower of onion, *Allium cepa*. (Source: Darrell Rainey.)

Cross-pollination is essential for producing hybrid seed with male-sterile lines. The pollen must be transferred from the male plants to the female (male-sterile) plants which produce the desired seed. Most growers plant two rows of male plants alternating with four rows of male-sterile (female) plants. The number of male rows is kept to a minimum because they take up space but do not produce the desired seed. Male rows are cut and removed before harvest so that they will not contaminate the desired seed.

Onion Pollinators

At least 276 species of insects are known to visit onion flowers; of these, honey bees, syrphid flies, halictid bees, and drone flies are the most important pollinators (Bohart *et al.*, 1970). When onion breeders want seed from a specific plant, they sometimes place a bag over the umbels and introduce flies to pollinate the florets. Mayer *et al.* (1993) tried to increase fly numbers by placing buckets of rotting meat

Table 39.1. Recommended bee densities for onion.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
2–15 (5–37)	McGregor (1976)
3–4 (7.4–10)	Levin (1986)
4–12 (10–29.6)	Mayer *et al.* (1993)
6.7 (16.5)	**Literature average**

around seed onion fields, but they had little success. Alfalfa leafcutting bees have not performed satisfactorily as onion pollinators (Mayer *et al.*, 1993). Only honey bees can be provided in the large and manageable quantities needed for commercial-scale seed production. Wind does not significantly aid pollination (Erickson and Gabelman, 1956).

Honey bees are usually adequate pollinators of open-pollinated onions because all of the plants produce nectar and pollen. However, in hybrid seed production using male-sterile plants (that do not shed pollen), only nectar-collecting bees will move freely from female to male plants, transferring pollen as they go. Pollen-collecting bees concentrate on the male rows and do not visit and cross-pollinate the male-sterile rows. To growers' frustration, honey bees sometimes visit neither open-pollinated nor hybrid flowers.

Onion seed yields, particularly hybrid seed yields, depend heavily on pollinator activity for good seed set. However, onion is not especially attractive to bees, and bees readily ignore it to concentrate on more attractive plants nearby (Gary *et al.*, 1972). Pollinator numbers are frequently low, even in fields well supplied with bee colonies, and pollination is often a limiting factor in onion seed production (Waller, 1983). The unpalatableness of onion nectar may be traced to its high levels of potassium or sugars (Mayer *et al.*, 1993). Nitrogen soil fertility does not seem to affect the quality of onion nectar. Some onion varieties are inherently more attractive to honey bees than others, and generally those most attractive produce the most seed (Hagler and Waller, 1991). This suggests that onion breeders may do well to select for stocks that are more attractive to bees.

Mayer *et al.* (1993) could not identify any cultural or bee management practices for increasing the attractiveness of onion flowers to honey bees. Thus, growers' only alternative is to use a heavy population of bees. However, simply placing hives in the field does not guarantee that bees will work the crop. Growers generally place 5–15 colonies of bees acre^{-1} (12.4–37 ha^{-1}) in or next to seed fields at the time of flowering. One recommendation calls for about two colonies acre^{-1} (5 ha^{-1}) placed after flowering has begun, then adding another two acre^{-1} at 3–4 day intervals to take advantage of the behaviour of inexperienced bees (see Chapter 7, page 54); however, when Mayer *et al.* (1993) tried this method they found no increase in the number of honey bees visiting onion.

Chapter 40

Peach and Nectarine

The smooth-skinned nectarine is a mutant variation of the fuzzy-skinned peach (*Prunus persica*). Occasionally, nectarine-like fruit develop on peach trees, and vice versa.

Flowering

The pink or reddish flower of peach and nectarine has five oval petals, is 1–1½ in (25–40 mm) across, and occurs in clusters along branches. There are 15–30 stamens surrounding a single erect pistil that leads to a single ovary (Fig. 40.1). The ovary contains two ovules but after fertilization only one develops, thus the fruit develops asymmetrically. Nectaries occur at the base of the corolla. Many types of insects visit peach for nectar and pollen.

The stigma is receptive as soon as the flower opens and remains so for 4–7 days. Fruit-set is optimized if the flower is pollinated soon after it opens. The anthers shed pollen during the period of stigma receptivity.

Peach and Nectarine Pollination Requirements and Pollinators

Pollination in peach and nectarine is relatively simple because only one ovule per ovary needs to be fertilized. Varieties range from completely self-sterile to completely self-fertile. Because the self-sterile varieties require pollenizers and insect pollinators, few of them are grown any more regardless of their other good characteristics; this includes the varieties 'Alamar', 'Candoka', 'Chinese Cling', 'Hal-berta', 'J.H. Hale', 'June Elberta', and 'Mikado' (McGregor, 1976).

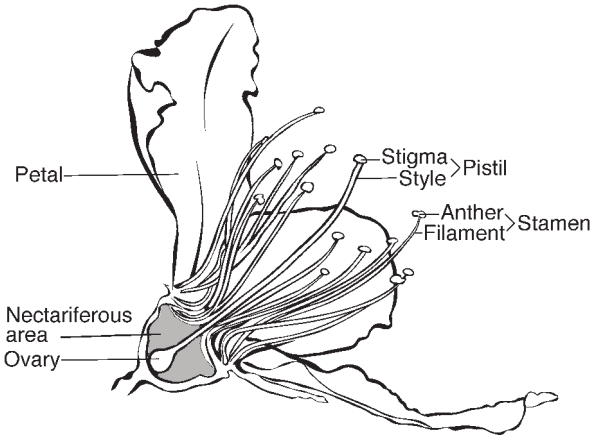


Fig. 40.1. Flower of peach or nectarine, *Prunus persica*. The flower has been partially dissected to reveal interior structures. (Source: (art) Darrell Rainey; (photo) Jim Strawser.)

However, even self-fertile varieties can benefit from insects transferring pollen from anthers to receptive stigmas, as shown in Table 40.1. Wind does not pollinate peach and nectarine. Most growers in the northwestern US move honey bees into their peach or nectarine orchards. Other growers believe that thinning peaches constitutes a greater problem than achieving adequate pollination. It is important to remember, however, that thinning is a moot point if the fruit is not set in the first place.

Table 40.1. Effect of excluding insects from flowers on percentage fruit-set in five self-fertile peach varieties (Bulatovic and Konstantinovic, 1960, cited in Free, 1993). Data are average percentage fruit-set over 2 years.

	'Alexander'	'Mayflower'	'Morteltini'	'Redbird'	'Vadel'
Flowers open	36.8	29.2	41.1	28.3	38.8
Flowers bagged	34.4	17.2	28.1	6.8	11.5

Table 40.2. Recommended bee densities for peach.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
0.2–0.3 (0.5–0.7)	Benner (1963)
For young trees: 0.4–0.8 (1–2)	Crane and Walker (1984)
For older trees: 1 (2.5)	
1–2 (2.5–5)	Levin (1986)
1 (2.5)	Mayer (1980)
0.08–1 (0.2–2.5)	Williams (1994)
1 (2.5)	Scott-Dupree *et al.* (1995)
0.8 (2)	**Literature average**

Chapter 41

Pear

Flowering

The pear (*Pyrus communis*) flower is about 1 in (2.54 cm) wide, has five white petals, and occurs in clusters along the branches (Fig. 41.1). There are five styles, and the stigmas mature earlier than the anthers. The style stands erect upon opening and the stamens bend so that the anthers are well below the receptive stigma. Later, the stamens stretch to their full length and the fully-mature anthers release pollen. Thus, the flower's behaviour discourages selfing. The ovary is made up of five compartments with two ovules each.

At first, only a few flowers open on a tree and, depending on the weather, more flowers open each day for 3–7 days. Pear produces abundant pollen but little nectar. The sugar content of pear nectar is low, 25% or less, depending on the variety. Therefore, bees avidly visit other plants that are more attractive, and most bee visitors on pear are pollen collectors.

Pear Pollination Requirements

Pear varieties range from self-fertile to self-sterile. Some are only partially self-fertile and benefit measurably from cross-pollination. Some varieties show different degrees of self-fertility in different regions and growing practices. For example, most growers of 'Bartlett' in California do not interplant pollenizers, but 'Bartlett' needs a pollenizer where it is grown in other areas of North America. It is prudent to interplant a pollenizer in an orchard unless the main variety is known to be self-fertile in one's particular area.

Most pear varieties are self-sterile and benefit from cross-pollination with another variety (Free, 1993). Fruit-set in the variety 'Anjou' is sometimes difficult, but this can be overcome partly with proper

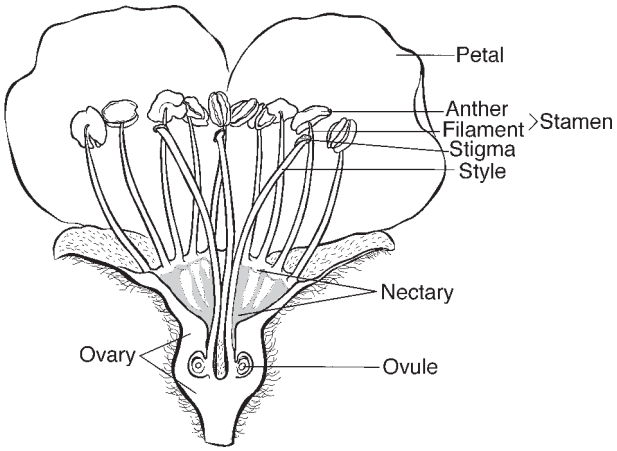


Fig. 41.1. Flower of pear, *Pyrus communis*. (Source: Darrell Rainey.)

interplanting. 'Anjou' should be planted in 2–3 solid rows, alternated with 2–3 rows of 'Bartlett' and 2–3 rows of a third commercial variety (Mayer *et al.*, 1986). Table 41.1 lists some suitable pollenizers. About 6–7% of the flowers must be set in order to produce a good crop.

Pear Pollinators

Many types of bees and flies visit pear, but honey bees are the only practical pollinator. Honey bees do not prefer pear, and honey bee management centres on overcoming this liability.

High honey bee numbers can help increase bee visitation to flowers through increased competition. Humphry-Baker (1975) recommends for British Columbia, 'twice the bee hives per acre in pears than in other fruits'.

A second way to increase honey bee efficiency is to use inexperienced bees (see Chapter 7, page 54). Mayer (1994) tested a method for increasing the number of inexperienced bees in an orchard. At 0–10% bloom, 14 orchards were initially stocked at two hives acre^{-1} (5 ha^{-1}). Four more colonies were moved into one end of each orchard at about 50% bloom; the other end was left as an untreated check. On the day after moving in the extra hives, in 9 of 14 orchards the number of bees per tree was higher in the half of the orchard receiving extra hives, but there were no differences on day two. In 10 of 14 orchards, the percentage fruit-set was higher in the half of the orchard receiving extra hives. Thus, it seems that the benefit of inexperienced bees lasted only one day, but it was enough to significantly increase fruit-set.

Table 41.1. Some pear varieties and suitable pollenizers. Blank boxes indicate suitable pollenizer combinations. A '0' indicates varieties that are not suitable pollenizers for each other. An 'X' indicates that the variety is partially self-fruitful but should not be planted in solid blocks.

Pollen source variety	Variety pollinated: Red Clapp	Bartlett	Max-Red Bartlett	Red Sensation	D'Anjou	Red D'Anjou	Du Comice	Seckels	Packham's Triumph	Bosc	Bronze Beauty Bosc	Concorde	Hosui	Kosui	Shinseiki	20th Century
Red Clapp	0															
Bartlett		X	X	X				0								
Max-Red Bartlett		X	X	X				0								
Red Sensation		X	X	X				0								
D'Anjou					0	0										
Red D'Anjou					0	0										
Du Comice							X									
Seckels		0	0	0				0								
Packham's Triumph					0	0			0							
Bosc										0						
Bronze Beauty Bosc											0					
Concorde												0				
Hosui													X			
Kosui														0		
Shinseiki															X	
20th Century																X

Honey bee attractants may be helpful in a crop like pear that is not attractive to honey bees. Bee-Scent®, a Nasonov pheromone-based attractant, increased honey bee visitation in Washington, USA for 24 h post-treatment in 'Bartlett' and 'Bosc', but not in 'Anjou'. Bee-Scent® increased fruit-set by 23% in 'Bartlett' and by 44% in 'Anjou'. Bee-Scent Plus® increased fruit-set by 44% in 'Bartlett' (Mayer *et al.*, 1989a). Queen mandibular pheromone (QMP)-based attractants increased honey bee visitation in 'Anjou' and 'Bartlett' in Washington and British Columbia and increased fruit diameter, all of which translated to a US$427 acre^{-1} (US$1055 ha^{-1}) increase in farmgate revenue (Currie *et al.*, 1992b). In another study, QMP-based attractant did not increase honey bee numbers nor fruit-set in 'Anjou', but did increase fruit size by 7% which translated to a US$162 acre^{-1} (US$400 ha^{-1}) increase in farmgate revenue (Naumann *et al.*, 1994b).

Table 41.2. Recommended bee densities for pear.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
2 (5)	Humphry-Baker (1975)
0.5–2 (1.2–5)	McGregor (1976)
1–2 (2.5–5)	Levin (1986)
2 (5)	Mayer *et al.* (1986)
0.4–2 (1–5)	Kevan (1988)
2 (5)	British Columbia Ministry of Agriculture, Fisheries, and Food (1994)
0.4–2 (1–5)	Williams (1994)
1–2 (2.5–5)	Scott-Dupree *et al.* (1995)
1.5 (3.7)	**Literature average**
Other measure	
10–15 honey bees per tree min^{-1}	Mayer *et al.* (1990)

There has been keen interest in identifying other bee species that do not share honey bees' disinterest in pear. However, the search has not been fruitful. A solitary bee, *Andrena nivalis*, in western North America visits pear and probably is an effective pollinator when it occurs in large numbers, but its active season does not always coincide with pear bloom (Miliczky *et al.*, 1990). Spring-introduced horned-face bees, *Osmia cornifrons,* and blue orchard bees, *O. lignaria propinqua,* rarely visit pear flowers in south central Washington and instead visit other flowering plants (D.F. Mayer, unpublished data). The incidence of flower visitation by commercially reared and hived bumble bees totalled only three bees over three years in an orchard of 'Anjou', 'Bartlett', and 'Bosc' pears in Washington (Mayer *et al.*, 1994a). Some speculate that flies are good pollinators of 'Anjou', but there is no research to support this.

Chapter 42

Pepper (Bell, Green, Sweet)

Flowering

The pepper (*Capsicum annuum*) flower is $\frac{3}{8}$–$\frac{5}{8}$ in (1–1.5 cm) across, has five stamens, one stigma, and a bell- or wheel-shaped white corolla (Fig. 42.1). The flower opens shortly after sunrise and stays open less than 1 day. The stigma is receptive before the anthers release pollen. Anthers release pollen a few hours after the flower opens, but sometimes they never release pollen at all. The stigma can be either shorter or longer than the stamens; thus the flower may not self-pollinate even if it does release pollen. In other cases, the stigma touches the anthers and self-pollination occurs. The pepper flower produces nectar at the base of the ovary. Bees visit pepper for nectar and pollen, but they are easily distracted away to more attractive blooming plants. Nectar production varies across varieties (Rabinowitch *et al.*, 1993).

Pepper Pollination Requirements

Pepper is generally self-pollinating, but cross-pollination is also common. Cross-pollination is mandatory in those flowers in which the anthers never release pollen. Each seed requires one grain of pollen to be deposited on the stigma, and poorly pollinated stigmas will result in misshapen fruit. Pollination by hand, by a mechanical pollination device, or by alfalfa leafcutting bees increases fruit-set and yield even in naturally self-pollinating varieties (Rasmussen, 1985); thus, the activity of an external pollinating agent is beneficial.

The incidence of cross-pollination ranges from 5–24% (Lorenzetti and Cirica, 1974) to 58–68% (Murthy and Murthy, 1962). Such outcrossing is a liability in breeding programmes. The New Mexico (USA) Crop Improvement Association (1992) requires an isolation distance of 1 mile (1.6 km) for foundation seed and 0.25 mile (0.4 km) for

certified seed. One alternative to cumbersome isolation distances is to use insect-proof plant cages that ensure self-pollination in pepper (Bosland, 1993).

Male-sterile lines give the opportunity for producing hybrid seed which is known in other crops to give superior vigour and productivity. Male-sterility occurs in certain pepper varieties (Shifriss and Frankel, 1969), but most show only partial male-sterility (Breuils and Pochard, 1975). Compared to male-fertile plants, male-sterile plants produce lower volumes of nectar with smaller amounts of sugar, and bee visitation to male-sterile flowers is 4–5 times lower than in male-fertile flowers (Rabinowitch *et al.*, 1993). Rabinowitch *et al.* suggest that plant breeders could improve pollination rates by selecting for plants with attractive nectar, although the heritability of nectar characteristics in pepper is low. Hybrid seed production requires an external pollinating agent, such as honey bees, to transfer pollen from male-fertile to male-sterile lines. Anais and Torregrossa (1979) produced hybrid seed by alternating rows of male-fertile and male-sterile plants. However, honey bees cross between lines better when the varieties are interplanted in a chessboard pattern so that each row has plants of both lines (Kubišová and Háslbachová, 1991).

Cold night temperatures can be a limiting factor in pepper pollination by inducing a decrease in pollen fertility. The weight and size of fruits reared from 'Latino' plants maintained at 75.2/53.6°F day/night

Fig. 42.1. Flower of pepper, *Capsicum annuum*. (Source: Darrell Rainey.)

(24/12°C) were smaller than that of fruits reared at 86/68°F (30/20°C) (Mercado *et al.*, 1997). However, optimized pollination (by hand) of the cold plants increased slightly the number of seeds per fruit and fruit length, suggesting a small compensatory effect of optimized pollination under conditions of cold temperature.

Pepper Pollinators

Several types of bees visit pepper, but honey bees are the most common pollinator. Fruit-set is satisfactory in glasshouse production in The Netherlands during summer months when windows are open and many insects are visiting the plants. Pollination can be a problem in spring and autumn, but honey bees moved into glasshouses at these times increase fruit size and weight, seed number, and number of well-shaped fruits. Honey bee pollination is standard practice in glasshouse pepper production in The Netherlands (Ruijter *et al.*, 1991).

Honey bees readily visit and move between male-sterile 'Sivria 600' and male-fertile 'California Wonder' in glasshouse conditions in Czechoslovakia (Kubišová and Háslbachová, 1991). However, honey bees in the open concentrate on male-fertile lines to collect pollen (Breuils and Pochard, 1975).

Managed bumble bees can increase fruit weight, width, whole-fruit volume, seed weight, and speed of ripening in 'Plutona' in glasshouse conditions in Ontario, Canada. Bumble bees increase speed of ripening for 'Cubico' under similar conditions (Shipp *et al.*, 1994). The increased speed of ripening for both varieties probably translates into one additional flush of fruit over the course of a growing season.

Imported horned-face bees (*Osmia cornifrons*) are known to increase pepper yield in glasshouses in Denmark early in the season when pollination is historically poor, compared to pollination by a mechanical device or by natural self-pollination. However, the bees cannot increase their populations on pepper even when glasshouses are supplemented with flowering phacelia (*Phacelia tanacetifolia*) or currant (*Ribes* spp.). By mid-June there is no difference in fruit yield between plants pollinated mechanically, by bees, or by self-pollination (Kristjansson and Rasmussen, 1991).

Wind and rain do not pollinate pepper (Crane and Walker, 1984). Certain flies (*Calliphora* spp., *Lucilia* spp.) occasionally pollinate pepper (Breuils and Pochard, 1975). Unlimited visits by the drone fly *Eristalis tenax* were shown in glasshouse-grown 'Bell Boy' sweet pepper to increase the number of fruits in the 20–25 cm circumference category and in the 100–120 g weight category compared to that of plants caged to exclude pollinators (Jarlan *et al.*, 1997).

There are no published recommendations for honey bee densities in pepper. For bumble bees, the data of Shipp *et al.* (1994) support a glasshouse stocking rate of one hive (containing 24–77 bees) per 1600 ft^2 (150 m^2) of plants.

Chapter 43

Plum and Prune

Flowering

The most important plums commercially grown around the world are the European plum (*Prunus domestica*), Japanese plum (*P. salicina*), and hybrids of the Japanese plum. Prunes are simply plums with sufficiently high sugar content that they can be dried without removing the stone. The flowers of plum and prune are each about 1 in (2.5 cm) wide and have five petals, several stamens, one style with a two-lobed stigma, and an ovary with one compartment and two ovules, only one of which usually develops (Fig. 43.1). Stamens are longer, shorter, or the same length as the stigma depending on the variety. The stigma is receptive as soon as the flower opens, and the flower stays open for 3–5 days. Anthers usually release pollen only after the flower is fully open. Flowers soon drop if they are not pollinated. Flowers occur in clusters of 1–3 along new-growth branches. Nectaries are at the base of the style, and the quantity and concentration of nectar differ considerably among varieties. The flower is attractive to bees.

Plum and Prune Pollination Requirements

Plum varieties range from completely self-sterile to self-fertile, but most require cross-pollination with a suitable pollenizer (Table 43.1). European plums require a European pollenizer, and Japanese plums require a Japanese pollenizer. Some varieties require specific other varieties as pollenizers and will not set fruit unless those pollenizers are present in the orchard. Conversely, some varieties are cross-incompatible and will not set fruit when pollinated with the other's pollen. All varieties, even self-fertile ones such as 'Italian' and 'Stanley', need insects to transfer pollen to receptive stigmas.

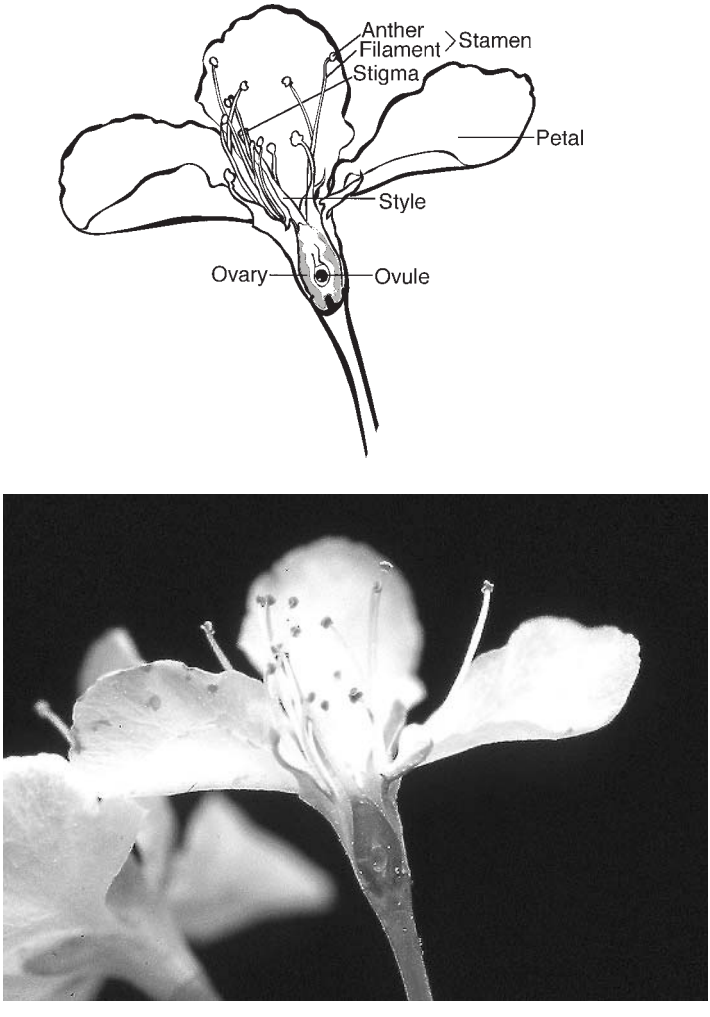


Fig. 43.1. Flower of plum, *Prunus* species. The flower has been partially dissected to reveal interior structures. (Source: (art) Darrell Rainey; (photo) Jim Strawser.)

With self-sterile varieties, one should interplant orchards in order to increase chances of bees visiting a pollenizer and main variety on the same foraging trip. The most common arrangement is to have a pollenizer as every third tree in every third row. It is important that the pollenizer blooms at the same time as the main variety.

A fruit-set of 15–20% should make a good crop; however, this is possible only in orchards with good pollenizer interplanting and high bee populations.

Table 43.1. Some plum and prune varieties and suitable pollenizers. Blank boxes indicate suitable pollenizer combinations. A '0' indicates varieties that are not suitable pollenizers for each other. An 'X' indicates that the variety is partially self-fruitful but should not be planted in solid blocks.

Pollen source variety	Variety pollinated: Shiro	Catalina	Black Amber	Imp. Duarte	Simka	Santa Rosa	Friar	Yakima	Damson	Early Italian	Double X French	Italian PRH 1	Stanley	Blufre	Empress	President
Shiro	X								0	0	0	0	0	0	0	0
Catalina		X							0	0	0	0	0	0	0	0
Black Amber			X						0	0	0	0	0	0	0	0
Imp. Duarte				0					0	0	0	0	0	0	0	0
Simka					X				0	0	0	0	0	0	0	0
Santa Rosa						X			0	0	0	0	0	0	0	0
Friar				0			0		0	0	0	0	0	0	0	0
Yakima	0	0	0	0	0	0	0	0								
Damson	0	0	0	0	0	0	0		X							
Early Italian	0	0	0	0	0	0	0			X						
Double X French	0	0	0	0	0	0	0				X					
Italian PRH 1	0	0	0	0	0	0	0					X				
Stanley	0	0	0	0	0	0	0						X			
Blufre	0	0	0	0	0	0	0							X		
Empress	0	0	0	0	0	0	0								0	
President	0	0	0	0	0	0	0									0

Plum and Prune Pollinators

Honey bees are the most important pollinator of plum and prune. They usually work the flowers well, especially in the morning. Honey bee attractants may be helpful under suboptimal pollination conditions such as poor weather, competing bloom, or when the bee-keeper is prevented from depositing hives in orchard interiors. Bee-Scent®, a pheromone-based attractant, increased honey bee visitation for 24 h post-treatment in 'President' plum, and Bee-Scent Plus® increased fruit-set by 88% (Mayer *et al.*, 1989a). Attractants are warranted only when existing populations of honey bees are not pollinating effectively; the first priority must be large bee populations in the orchards. Webster *et al.* (1985) showed in plum orchards that honey bee hives fitted with pollen traps fielded a higher proportion of pollen foragers compared to non-modified hives.

Table 43.2. Recommended bee densities for plum and prune.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
1 (2.5)	McGregor (1976)
1–2 (2.5–5)	Standifer and McGregor (1977)
1 (2.5)	Crane and Walker (1984)
2 (5)	Mayer *et al.* (1986)
1 (2.5)	Kevan (1988)
1 (2.5)	Scott-Dupree *et al.* (1995)
1.3 (3.2)	**Literature average**

The flight season of imported horned-face bees (*O. cornifrons*) coincides with plum bloom in Maryland (Batra, 1982). However, populations of non-managed bees are generally too small to support commercial pollination needs in orchard crops (Scott-Dupree and Winston, 1987).

Chapter 44

Raspberry

Flowering

The most important raspberries grown around the world are the European raspberry (*Rubus idaeus*), the red (*R. strigosus*) and black (*R. occidentalis*) wild raspberries, and the purple raspberry – a hybrid of the last two. Most flowers are perfect (Fig. 44.1), and each is about 1 in (2.54 cm) wide with 5–12 petals, ~90 stamens, and ~90 pistils each of which has an ovary and a slender style (Redalen, 1980; Jennings, 1988). Thus, raspberry is an aggregate fruit, like strawberry and blackberry, with many pistils developing together as a single mass. When the flower opens, the immature anthers are bent over the immature styles, but shortly thereafter the outer stamens bend away from the styles and release pollen. Anthers mature and release pollen from the edge of the flower inward, during which time the styles grow and receptive stigmas emerge from their tips. Only the innermost anthers have a chance to touch the outermost stigmas; this accomplishes selfing unless the stigmas had previously been cross-pollinated. Thus, both crossing and selfing are possible on the same flower. The petals begin to fall after one day of opening. A plant may be in various stages of flowering for 1–3 weeks. Raspberry is a rich source of nectar and pollen for bees.

Raspberry Pollination Requirements

Raspberry is moderately self-fertile, but its flowering behaviour gives ample opportunity for cross-pollination. Depending on the variety, cross-pollination with pollen from other varieties improves development of maternal tissues with an accompanying increase in fruit weight (Colbert and de Oliveira, 1990). Bees help deliver pollen evenly among all receptive stigmas, thus optimizing fruit weight and shape

Fig. 44.1. Flower of raspberry, *Rubus* species. (Source: Darrell Rainey.)

even in self-fertile varieties (Kühn, 1987). Because raspberry is an aggregate fruit, it requires multiple bee visits to adequately pollinate all the ovaries.

Raspberry Pollinators

Raspberry is very attractive to bees and other insects, and studies over the years have demonstrated the yield-enhancing effects of insect pollination (Johnston, 1929; Couston, 1963; McCutcheon, 1978). Honey bees and bumble bees are the most important pollinators.

In Québec, Canada, the number of developing ovaries and fruit weight increase as the number of honey bee visits per flower increases. Five or six honey bee visits, or ~150 accumulated bee seconds per flower, are necessary in order to optimize the number of fertilized ovaries and fruit weight. This is easily accomplished in one day of good bee activity. Honey bees are most efficient if they are collecting pollen as well as nectar, rather than nectar only (Chagnon *et al.*, 1991).

Table 44.1. Recommended bee densities for raspberry.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
0.2–0.8 (0.5–2)	Yakovleva (1975)
> 1 (> 2.5)	McGregor (1976)
> 1 (> 2.5)	Scott-Dupree *et al.* (1995)
0.8 (2)	**Literature average**
Other measures	
1 honey bee per 100 open flowers	McGregor (1976)
5–6 honey bee visits per flower	Chagnon *et al.* (1991)

The distribution of foraging honey bees in raspberry fields in British Columbia is uniform during warm, still weather, even if the hives are clumped at one end of the field. However, bees will concentrate on plants nearest their hives during overcast weather or wind. This can be a problem in British Columbia because raspberry blooms in June which is typically wet and cool. Distributing hives throughout a field may help, but this is labour intensive and the hives may intimidate labourers picking the earliest berries (Murrell and McCutcheon, 1977).

Bumble bees are excellent pollinators and make up about 60% of all insect visits to raspberry in Scotland. Compared to honey bees, bumble bees prefer the youngest flowers that contain the most pollen; honey bees visit old (pollen-poor) flowers and young flowers indiscriminately. Compared to honey bees, bumble bees forage for more hours in the day, tolerate more inclement weather, visit more raspberry flowers per minute, carry more raspberry pollen on their bodies, and deposit more pollen on raspberry stigmas (Willmer *et al.*, 1994). These advantages over honey bees are explained by bumble bees' greater body size and superior abilities for cool-weather foraging. Raspberry production is highest in cool-summer regions – Canada, northeastern Europe, and Scotland – thus, bumble bees deserve special attention as pollinators for this crop. However, natural populations of bumble bees are unpredictable and cultured bumble bees are expensive.

Natural populations of other non-honey bees are generally too small to support commercial pollination needs in raspberry (Winston and Graf, 1982).

Chapter 45

Soybean

Flowering

The soybean (*Glycine max*) inflorescence is a raceme of 1–35 white or purple florets, each about $\frac{3}{8}$ in (1 cm) long. A plant may have up to 800 florets. Each floret has a large standard petal, two narrow wing petals, and two keel petals that partially enclose ten stamens and the style (Fig. 45.1). The ovary contains 3–5 ovules; thus, each floret can potentially produce one bean pod. The flowering period lasts for up to six weeks, but individual florets bloom for only one day. Bees visit soybean for nectar and pollen, but flower attractiveness varies greatly by location. Soybean is an important source of honey in areas with good soils and warm climates (Erickson, 1982).

Soybean Pollination Requirements

Anthers release pollen and the stigmas are receptive before the flower opens; thus, self-pollination is the norm in soybean. In spite of automatic self-pollination, over 75% of flowers abort in some varieties (Erickson, 1982) which raises the question whether pollination is a limiting factor in soybean production.

Bee pollination has been shown in some cases to improve fruit-set and yield, but the benefits vary greatly across varieties and growing conditions. In some localities and varieties, the flowers never open, and with these self-pollination is the rule. In other regions the same variety's flowers may open, permitting an opportunity for bee pollination. In general, benefits from bee pollination are more evident in areas with poorer soils (Erickson, 1982). If bee activity improves yield in soybean, it is unclear whether it results from cross-pollination or from more effective selfing.

Natural cross-pollination in soybean averages less than 1% (Free, 1993). However, outcrossing was shown to average 0.09–1.63% and sometimes reaches 2.5% in 12 selected varieties grown in Arkansas, USA under optimum growing conditions and bee populations (Ahrent and Caviness, 1994).

Hybrid soybean lines can yield at higher levels than either parent line (McGregor, 1976), but producing commercial hybrids is difficult because of soybean's self-pollinating habit. Genetic male-sterility exists in soybean (Brim and Young, 1971); however, genetic male-sterility is unsuitable for developing commercial soybean hybrids (Erickson, 1982) so progress has been slow. Producing hybrids requires bees to move pollen between lines or from male-fertile to male-sterile plants.

Soybean Pollinators

Honey bees are the most notable insect pollinator of soybean. Honey bee pollination increased pod set and yield in 'Corsoy' and 'Hark', but not in 'Chippewa 64' in cage studies in southern Wisconsin, USA (Erickson, 1975a). In Missouri and Arkansas, the number of beans was 15% higher and the number of empty pods 18.6% lower in 'Pickett 71' caged with honey bees than in cages from which bees were excluded, but this did not necessarily translate into increased yield by weight. In soybean fields with honey bee hives nearby, yield was higher up to 109 yards (100 m) from the hives than it was at greater distances (Erickson *et al.*, 1978). But a separate study found no such

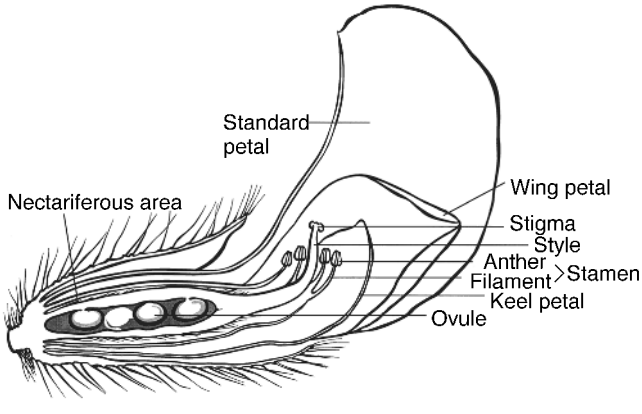


Fig. 45.1. Flower of soybean, *Glycine max*. (Source: Darrell Rainey.)

relationship between yield and distance from hives at distances of 13–535 yards (12–489 m) (Sheppard *et al.*, 1979).

If hybrid soybeans are developed on a practical scale, it will be important to use parental lines that are attractive to bees so that bees will visit and move pollen between plants. Bee attractivity data should be collected locally because soybean flowering characteristics vary geographically. In Wisconsin, the varieties 'Adams', 'Corsoy', 'Hark', 'Illini', 'Lincoln', 'Wayne', and 'Williams' are relatively attractive to bees (Erickson, 1975a,b,c). In Delaware, the varieties 'York' and 'Essex' rank highest in attractivity, and (unlike Wisconsin) 'Williams' ranks relatively low (Mason, 1979).

Supplemental bees are rarely, if ever, used for pollinating soybean in the field. This could change if production of hybrids becomes practical, in which case bees will be needed to transfer pollen between parent lines. Sheppard *et al.* (1979) consider 0.6 honey bee hives acre^{-1} (1.4 ha^{-1}) adequate to provide cross-pollination.

Chapter 46

Squash, Pumpkin and Gourd

Flowering

Squash, pumpkin, and gourd (*Cucurbita* species) plants are normally monoecious which means that there are both male and female flowers on the same plant (Fig. 46.1). Male flowers outnumber female ones by 3.5:1 to 10:1. Each flower is about 3 in (7.6 cm) wide. Each male flower occurs at the end of a slender stem and has three anthers. Each female flower occurs at the end of a short peduncle and has a thick style and a two-lobed stigma; the swollen ovary occurs at the base of the corolla and is divided into 3–5 sections. Male flowers produce nectar and pollen, and female flowers produce nectar. Female flowers produce more nectar and attract more bees compared to male flowers (Nepi and Pacini, 1993). The pollen grains are large and well suited to insect transport. Flowers open early in the morning and close around noon of the same day, never to reopen (Skinner and Lovett, 1992; Nepi and Pacini, 1993).

Squash, Pumpkin and Gourd Pollination Requirements

Because these plants have separate male and female flowers, some agent – usually bees – is necessary to transfer pollen from male to female flowers. Squash plants caged to exclude pollinators produced no fruit in west Tennessee, USA (Skinner and Lovett, 1992). Wind does not pollinate *Cucurbita*. Ovules are fertile only during the flowering period or on the day before in the squash variety 'Greyzini' in Italy. Pollen viability in a newly opened male flower is about 92% but by the time it closes that same morning the viability will have dropped to 75%, and by the next day it will be only 10% (Nepi and Pacini, 1993). Thus, it is important for a female flower to be pollinated as early as possible on the day it opens while pollen is still viable.

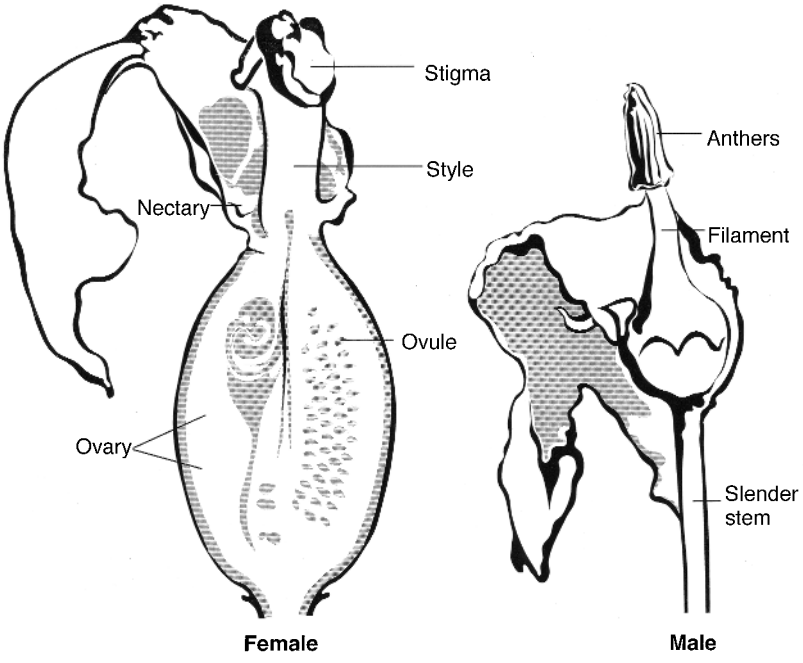


Fig. 46.1. Flower of squash, which is representative of other *Cucurbita* species such as pumpkin and gourd. The dissected female flower is on the left and the male on the right. (Source: (art) Darrell Rainey; (photo) Keith S. Delaplane.)

Early bee activity is even more important on hot days when flowers close early. Rate of fruit-set is similar in selfed or crossed fruit, but cross-pollination produces heavier fruit as shown in squash in India (Girish, 1981).

Different varieties of the same species, and even different species, can cross each other in *Cucurbita* (Table 46.1). Even with incompatible species the pollen of one may stimulate parthenocarpic (seedless) fruit development in another; this phenomenon does not result in contaminated seed, but it does reduce total seed yield (Free, 1993). Thus, different varieties and species of *Cucurbita* must be isolated from each other in order to produce large quantities of pure seed.

Squash, Pumpkin and Gourd Pollinators

Squash bees and honey bees are the most important pollinators of *Cucurbita* species. Squash bees (*Peponapis pruinosa*) are excellent pollinators of squash and pumpkin. Compared to honey bees, they make more contact with reproductive parts of a flower, work faster, and work earlier in the morning. However, squash bees are no more efficient than honey bees at setting fruit in spite of their desirable behaviours (Tepedino, 1981). Nevertheless, growers should always encourage wild squash bee populations (see Chapter 10, pages 99 and 103). Supplemental colonies of honey bees are unnecessary where squash bees occur in high numbers.

Honey bees work *Cucurbita* flowers and effectively pollinate the crop (Table 46.2). They are the most numerous bee visitor to summer squash in west Tennessee, and they freely visit male and female flow-

Table 46.1. Cross-compatibility of certain *Cucurbita* species (Whitaker and Davis, 1962). A '+' indicates species that will cross with each other, and a '−' indicates species that will not cross.

	C. maxima (winter squash)	*C. mixta* (cushaw squash)	*C. moschata* (pumpkin)	*C. pepo* (summer squash)
C. maxima (winter squash)	NA	−	−	−
C. mixta (cushaw squash)	−	NA	+	−
C. moschata (pumpkin)	−	+	NA	+
C. pepo (summer squash)	−	−	+	NA

NA, not applicable.

Table 46.2. Effects of increasing bee visits to *Cucurbita* species flowers.

Location	Bee(s) tested	Conclusion	Reference
Illinois, USA	Honey bee	As number of bee visits to a pumpkin flower increases from 1 to 12, fruit-set increases from 6% to 64% and number of seeds per fruit increases from 273 to 366.	Jaycox *et al.* (1975)
India	Asian honey bee	As number of bee visits to a summer squash flower increases from 1 to 7, fruit-set increases from 30% to 100%.	Girish (1981)
Utah, USA	Honey bee, squash bee	One bee visit results in 22% fruit-set in summer squash, but flowers with numerous visits have 66% fruit-set.	Tepedino (1981)

ers. Honey bees with large pollen loads are often seen visiting female flowers (Skinner, unpublished report). However, honey bees are generalists and they readily move to any competing bloom that offers richer reward than *Cucurbita*. This is a problem in the southeastern US where wild gallberry, a rich source of nectar, blooms in competition with early squash. This is a situation where honey bee attractants may help focus bees on the crop (see Chapter 7, page 58); however attractants have a mixed record with *Cucurbita* species (Margalith *et al.*, 1984; Loper and Roselle, 1991; Schultheis *et al.*, 1994). Another way to deal with competing bloom is to increase the density of honey bee hives so that competition for nectar and pollen forces bees to forage on the crop. In Georgia, competition from wild bloom is less of a problem in fall plantings of squash.

Table 46.3. Recommended bee densities for squash, pumpkin and gourd.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
1 (2.5)	Hughes *et al.* (1982)
0.04–3 (0.09–7.4)	McGregor (1976)
0.8–1.6 (2–4)	Goebel (1984)
1–2 (2.5–5)	Levin (1986)
0.4–3.2 (1–8)	Kevan (1988)
1–3 (2.5–7.4)	Scott-Dupree *et al.* (1995)
1–2 (2.5–5)	Skinner (1995)
1.5 (3.8)	**Literature average**
Other bees	
1 squash bee per 20 flowers	Derived from Tepedino (1981)

Skinner and Lovett (1992) found that bumble bees were more efficient than honey bees at promoting good fruit-set in western Tennessee. Six of eight (75%) single bee flower visits by bumble bees resulted in whole fruit, whereas five of 16 (31%) single bee visits by honey bees resulted in whole fruit. However, in normal conditions and with adequate bee populations, every flower is visited many times, probably by more than one bee species, and fruit-set is very good.

Fruit-set and seed number increase as the number of bee visits to flowers increases (Table 46.2). This is due to the fact that seed formation increases as the number of pollen grains deposited on a stigma increases (Winsor *et al.*, 1987). Thus, large bee populations help ensure maximum flower visitation, pollen deposition, and crop yield.

Other wild solitary bees will visit squash in Tennessee, namely *Agapostemon virescens*, *Augochlora pura*, *Dialictus* sp., *Halictus* sp., *Triepeolus remigatus*, and *Mellisodes bimaculatus* (Skinner, unpublished report). These bees probably contribute to squash pollination, but their relative efficiency is unknown.

Chapter 47

Strawberry

Flowering

Strawberry (*Fragaria* x *ananassa*) flower clusters occur on a series of double branches with a flower in the crotch of each branch. The first flower is the *primary* flower; the next two are *secondary* flowers, and the next four are *tertiary* flowers. Primary flowers produce the largest fruit. The flowers are perfect in the most important commercial varieties, but some varieties have exclusively female flowers, exclusively male flowers, flowers with only a few stamens, or flowers with non-functioning stamens. Strawberry is an aggregate fruit like raspberry which means that each flower has many pistils that develop together as a single mass.

The flower is white and 1–1½ inches (2.5–3.8 cm) across. Each perfect flower has five petals, many pistils and styles, and 24–36 stamens (Fig. 47.1). Primary flowers have about 350 stigmas, secondary flowers have about 260, and tertiary flowers have about 180 (Darrow, 1966). Stamens become deep yellow when they have viable pollen. Nectar forms pools at the base of the outermost pistils. Stigmas become receptive before the anthers of the same flower release pollen; thus the flower's behaviour encourages cross-pollination. Pollen is not released until the flower has been open for a while and the anthers have begun to dry. When the drying anthers finally open, pollen bursts from them under tension and scatters across the numerous stigmas. Thus, self-pollination is possible. Once released, pollen stays viable for several days. Pollination is most likely to happen during the first 4 days after the flower opens (McGregor, 1976), but some flowers start to dry by the second day (Connor, 1970). Fertilized ovules stimulate the surrounding tissue to begin growing. Non-fertilized ovules do not grow and if there are many of them the berry will be misshapen, if it develops at all. Strawberry flowers produce nectar and pollen, but they are not always attractive to honey bees.

Strawberry Pollination Requirements

Most commercial varieties are self-fertile, and the pollen-scattering action of the anthers promotes self-pollination. However, every pistil in the aggregate flower must be pollinated in order to form a perfect berry, and self-pollination cannot service every pistil. Thus, wind and bees are important supplemental pollinators. Varieties differ considerably in their responsiveness to different modes of pollination. In a comparative study of strawberry genotypes (Żebrowska, 1998), the variety 'Redgauntlet' and the breeding clone B-320 were highly self-pollinating, 'Dukat' less so, and 'Paula' least of all. 'Dukat' was the most responsive to wind pollination, while 'Paula' was the most

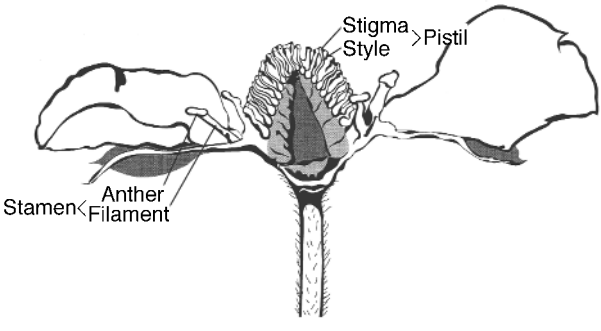


Fig. 47.1. Flower of strawberry, *Fragaria* x *ananassa*. The flower in the photograph has been partially dissected to reveal interior structures. (Source: (art) Darrell Rainey; (photo) Jim Strawser.)

Table 47.1. Effectiveness of honey bees as pollinators of strawberry (from data cited by Free, 1993).

Measurement	Effect (**average value** ± standard deviation)
Fruit-set	Increase by 25%
Yield	Increase by 18–100% (**45** ± 36.7%)
Malformed fruit	Decrease by 9–41% (**25** ± 13.5%)
Culled fruit	Decrease by 49%
Large fruit	Increase by 7–16% (**11.5** ± 6.4%)

responsive to insects. Certain morphological characteristics of the flowers are associated with high levels of self-pollination, namely, relatively long pollen grains and long stamens (Żebrowska, 1998). Long stamens, as occurring in 'Early Midway' (5.2 mm), are capable of shedding pollen more effectively on to the pistils below them than are shorter stamens, as in 'Surecrop' (2.5 mm) (Connor and Martin, 1973). Poor distribution of pollen on to stigmas results in small, misshapen, devalued fruit called *nubbins*.

Strawberry Pollinators

Strawberry is pollinated by self, wind, and bees. The relative contribution of each varies by variety, weather, and bee population size. On average, self-pollination accounts for 53% of fruit development; wind adds an additional 14% (= 67%), and bees add another 24% (= 91%) (Connor and Martin, 1973). Self-pollination is more difficult in varieties with short stamens, and for these the pollinating action of bees is more important.

Honey bee visitation improves fruit yield and quality in strawberry in spite of the plant's self-pollinating habit (Table 47.1, Antonelli *et*

Table 47.2. Recommended bee densities for strawberry.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
5–10 (12.4–25)	McGregor (1976)
0.8 (2)	Kevan (1988)
1 (2.5)	Williams (1994)
0.5 (1.2)	Scott-Dupree *et al.* (1995)
3.5 (8.6)	**Literature average**
Other measures	
16–19 honey bee visits per flower	Skrebtsova, 1957
1 honey bee colony per 10,800 ft^2 (1000 m^2) of glasshouse	Matsuka and Sakai (1989)
≥ 4 honey bee visits per flower	Chagnon *et al.* (1989)

al., 1988). Almost every honey bee visiting a strawberry flower contacts the stigmas and anthers (Free, 1968b); thus bees help distribute pollen to all pistils, which promotes a well-shaped fruit.

It takes many bee visits to spread pollen evenly and to optimize fruit-set and shape. In Russia, 16–19 honey bee visits per flower are considered adequate, and fruit-set is optimized at 20–25 visits (Skrebtsova, 1957). With 'Veestar' in Québec, Canada, most pollination is accomplished during the first 40 cumulative seconds of honey bee visitation which translates to the first four bee visits. Nearly 100% of the pistils are pollinated after six bee visits. Bee activity is especially important in the large primary flowers which have many stigmas and produce the best fruit. There is a higher rate of pollination by wind and gravity in the secondary and tertiary flowers that have fewer stigmas (Chagnon *et al.*, 1989). The variety 'Houkou-wase' in Japanese glasshouses requires 11 honey bee visits per flower to achieve adequate fruit-set (Kakutani *et al.*, 1993).

Weather conditions are often poor for bee activity during early-spring strawberry bloom. The best way to compensate for this is with imported honey bee hives. This is especially important in large plantations (de Oliveira *et al.*, 1991). Maximum bee activity in Michigan occurs from 10 a.m. to 3 p.m. and at average temperatures of 65–79°F (18–26°C) (Connor, 1972).

In glasshouse strawberry production in Japan, growers bring in honey bee hives when plants have achieved about 1–2 blooms each. Five-frame Langstroth-style hives are the norm, and the stocking rate is one colony per 10,800 ft^2 (1000 m^2) of glasshouse. Bee density is doubled with newer strawberry varieties that produce less pollen (Matsuka and Sakai, 1989).

Many insects visit strawberry. The most important insect pollinators of strawberry in Utah are honey bees, two species of solitary orchard bees (*Osmia* spp., see Chapter 12), a third solitary bee (*Halictus* sp.), and two species of pollinating flies (*Eristalis* spp.) (Nye and Anderson, 1974). Honey bees are the most numerous visitor to strawberry in Québec, followed by flies (Syrphidae) and solitary bees (Halictidae) (de Oliveira *et al.*, 1991). The relative abundance of bees by family in Michigan is Halictidae (49–52%), Apidae (31–35%), Andrenidae (14–20%), and Megachilidae (0–1%) (Connor, 1972). The pollinating fly *Eristalis cerealis* is mass-reared and used to pollinate glasshouse strawberry in Japan (Matsuka and Sakai, 1989). Bumble bees are rarely numerous on strawberry (Free, 1968a).

Bee species behave differently on strawberry flowers. In Québec, honey bees concentrate on the tip of the pistil mass whereas native bees concentrate on the base. Thus, pollen distribution and fruit quality are optimized when a diversity of bee species visits strawberry flowers (Chagnon *et al.*, 1993).

Chapter 48

Sunflower Seed

Flowering

Some sunflower (*Helianthus annuus*) plants have a primary flower head and one or more secondary heads, but commercial varieties usually have only one primary head. The primary head has 1000–4000 florets, and a secondary head has 500–1500 florets. The colourful outer *ray florets* are sterile with neither stamens nor a pistil. The less-showy inner florets are perfect, and each contains stamens and a pistil (Fig. 48.1). Each pistil has one ovary containing one ovule. Each floret releases pollen before its stigma is receptive, and florets are frequently self-incompatible.

Each floret is open for at least 2 days. On the first day, the stamens elongate above the top of the corolla and the anthers release pollen. By the second day the stigma has elongated to a point above the senescing male parts, and its inner receptive surfaces open to receive pollen. Thus, the flower has a male stage on day one and a female stage on day two, a behaviour which discourages selfing. Nectar production from nectaries at the base of the floret is highest during the male stage but persists a little into the female stage. Florets open from the head periphery inwards, so for most of its flowering career a head has unopened florets in the middle, surrounded by a ring of florets in the male stage, then a ring of florets in the female stage, a ring of withered florets, and finally the ray florets. One consequence of this pattern is that the centremost florets have the lowest probability of being pollinated because the ratio of male to female florets is decreasing with time (Goldman, 1976). Each head flowers for 5–10 days. Florets wither quickly if pollination is good. If not, florets will stay fresh for up to two weeks and the stigmas curl back and touch their own floret's pollen. Thus, selfing becomes possible, but the likelihood of seed set decreases with time (Radaeva, 1954). Sunflower nectar and pollen are very attractive to bees.

Sunflower Pollination Requirements

Some sunflowers are self-fertile which means that florets can set seed when they are pollinated with pollen from the same flower head. Other varieties are self-sterile and require pollen from another plant. Within-head selfing usually results in lower seed set, smaller seeds, lower oil content, and a lower germination rate compared to crossing (McGregor, 1976). Thus, cross-pollination is advantageous except in highly self-fertile varieties.

Growers can take advantage of increased productivity by using hybrid seed. Hybrid sunflowers are produced by crossing male-fertile lines with male-sterile lines. Hybrid seed is produced and harvested only from the male-sterile plants. In seed fields, blocks of male-fertile plants are interplanted with blocks of male-sterile plants. It is in the growers' best interest to maximize the number of male-sterile (seed-producing) rows. In experimental plantings of 5:5 or 3:3 male-sterile to male-fertile rows in Arizona, USA, seed set was decreased in rows further from pollen-bearing male-fertile plants (DeGrandi-Hoffman

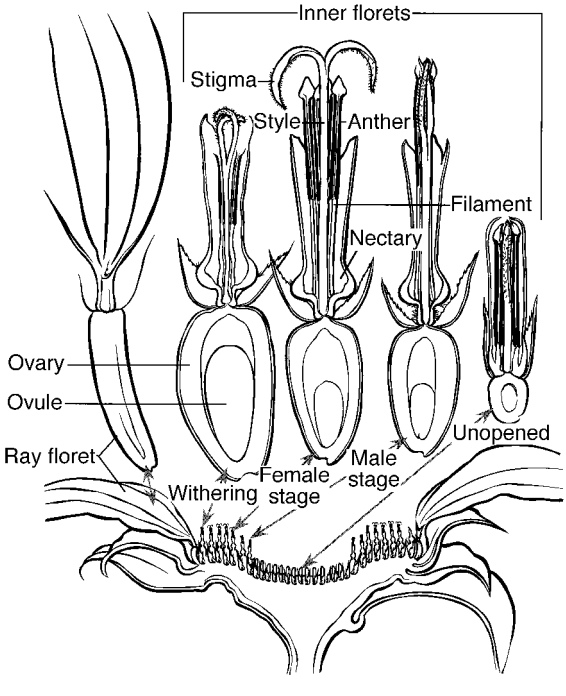


Fig. 48.1. Inflorescence of sunflower, *Helianthus annuus,* and detail of individual floret. (Source: Darrell Rainey.)

and Martin, 1993); in spite of this, it is generally thought that uniform ratios like these take up too much growing space with male-fertile plants. Seed set and yield can be optimized at plantings of 8:2 male-sterile : male-fertile rows (Delaude and Rollier, 1977; Delaude *et al.*, 1979).

Sunflowers grown from hybrid seed usually have a high degree of self-fertility. However, they are not necessarily self-pollinating and bees are still helpful for transferring pollen to receptive stigmas. Honey bee pollination increased seed yield by 30% and oil content of seed by 6% in hybrid varieties with intermediate levels of self-fertility (Furgala *et al.*, 1979). In Canada, most hybrid varieties are highly self-fertile and honey bees are not rented for pollination (Scott-Dupree *et al.*, 1995).

Sunflower Pollinators

Honey bees are the most important pollinator of sunflower. However, many bee species visit sunflower for nectar and pollen, pollinate the crop and, at least in self-sterile varieties, increase yield (Table 48.1).

Most honey bees visiting sunflower are collecting nectar, not pollen (Fell, 1986). But even nectar foragers become amply dusted with pollen which they carry to subsequent flowers. Flowers produce nectar in both the male and female stage. Thus, nectar-gathering bees

Table 48.1. Effectiveness of bees as pollinators of self-sterile sunflower.

Results	Reference
Fields stocked with 1 honey bee hive acre^{-1} (2.5 ha^{-1}) produced almost twice as much seed per acre compared to fields 3 miles (4.8 km) from hives.	Furgala (1954)
Heads caged without bees yielded 315 g seed; heads exposed to bees yielded 995 g; and heads exposed to bees plus supplemental manual pollination yielded 1000 g.	Luttso (1956)
Plots of 'Advance' caged without bees yielded 312 lb seed acre^{-1} (349 kg ha^{-1}); plots caged with bees yielded 602 lb acre^{-1} (675 kg ha^{-1}), and open plots yielded 932 lb acre^{-1} (1044 kg ha^{-1}).	Alex (1957b)
Seed yield increased 5–6 times, and oil content of seed increased 25% in plots exposed to honey bees compared to plots isolated from insects.	Schelotto and Pereyras (1971)
Open plots of male-sterile 'CMS 234A' accessible to bees and other insects yielded 25.4 g filled seeds while plots caged to exclude insects yielded 5.2 g filled seeds.	Rajagopal *et al.* (1999)

Table 48.2. Recommended bee densities for sunflower.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
0.4–1 (1–2.5)	McGregor (1976)
1–2 (2.5–5)	Levin (1986)
0.4 (1)	Free (1993)
0.4–1.6 (1–4)	Williams (1994)
0 (for self-fertile Canadian hybrids)	Scott-Dupree *et al.* (1995)
0.9 (2.1)	**Literature average**
For hybrid seed production	
0.5–4 (1.2–9.6)	Skinner (1987)
Other measure	
1 honey bee per head throughout the day	McGregor (1976)

are the most important pollinators because they are most likely to visit both flower stages. Honey bees prefer some varieties over others (Skinner, 1987). The varieties 'Arrowhead', 'Mingren', and 'Peredovik' received more bee visits than did 'Commander' (Goldman, 1976), and the variety 'Fleury' had both the highest nectar sugar concentration and rate of bee visitation (Schaper, 1998). The florets of some varieties are too deep for honey bees to reach the nectaries (Sammataro *et al.*, 1983). Plant breeders may benefit by selecting for plants with accessible florets or higher nectar production in female flowers.

It is important to have large numbers of bees to transfer pollen to male-sterile flowers in hybrid sunflower seed production. Honey bees visit male-sterile and male-fertile plants equally well in both summer and autumn in Arizona. Only 6.5–12.8% of the honey bees visiting male-sterile flowers have pollen loads on their legs, indicating that they had first visited male-fertile plants. However, bees can pick up sunflower pollen on their bodies at the hive from contact with foraging nestmates, and this helps ensure cross-pollination (DeGrandi-Hoffman and Martin, 1993). Seed set in sunflower tends to be higher in plants nearest to bee hives (McGregor, 1976). Thus, bee hives should be well dispersed throughout a field.

Numerous solitary bee species, some of which are sunflower specialists, visit and pollinate sunflower (Parker, 1981; Minckley *et al.*, 1994). Solitary bees may contribute to sunflower pollination, but perhaps less so than in other crops. Solitary species preferentially collect pollen and this may limit their activity on the seed-bearing male-sterile flowers in hybrid seed fields. DeGrandi-Hoffman and Martin (1993) point out that large numbers of solitary bees on male-fertile flowers may repel honey bees which, in turn, reduces the in-hive transfer rate of pollen and subsequent cross-pollination of male-sterile flowers.

Chapter 49

Tomato

Flowering

The tomato (*Lycopersicon esculentum*) flower is pendulous, about $\frac{3}{4}$ in (2 cm) in diameter and perfect, containing both stamens and a pistil. There are six yellow petals and six stamens that unite at their anthers to form a cone surrounding the pistil (Fig. 49.1). Inside the pistil is a five- to nine-chambered ovary. The style may be shorter than the tip of the anther cone or longer, depending on the variety. The stigma is receptive from 1–2 days before to 4–8 days after its own flower releases pollen; thus cross-pollination is possible. However, anthers release pollen inwardly towards the style, and vibration-assisted self-pollination is the norm especially in short-style varieties. In long-style varieties, the downward posture of the flower promotes self-pollination by gravity. The anther cone releases pollen around the stigma at the slightest vibration, whether from wind or insects. Tomato flowers produce pollen but little or no nectar.

Tomato Pollination Requirements

Tomato is self-fertile, and fruit-set is similar in self- or cross-pollinated plants (Free, 1993). The tomato flower must be shaken or vibrated in order to release pollen and self-pollinate. Natural cross-pollination in commercial varieties is low, ranging from 0.07% in California (Groenewegen *et al.*, 1994) to 12% in Mexico (Richardson and Alvarez, 1957) and is more common in long-style varieties because the stigma is more accessible to foreign pollen. Pollination can be a limiting factor in wind-free glasshouses with long-style varieties because they are not as easily self-pollinated (Wenholz, 1933).

Each seed requires one grain of pollen, and small misshapen fruit will result if the pollen transfer rate to stigmas is poor. The size and

weight of fruit increase as the number of developing seeds increases. Fruit-set and the number of seeds per fruit increase the more often a flower is pollinated, up to four times (Verkerk, 1957).

Male-sterility exists in tomato and is used to produce hybrid seed. This requires cross-pollination, but neither wind nor mechanical vibrators can cross-pollinate male-sterile flowers (McGregor, 1976). Thus, insects are necessary for hybrid seed production. Rate of crossing quickly decreases as the distance from the pollen source increases (Currence and Jenkins, 1942), and little pollen is transferred beyond 98 ft (30 m) from its source (Quiros and Marcias, 1978).

Tomato Pollinators

Wind and insects provide the vibrating action necessary for self-pollination under field conditions. But these natural phenomena may not result in maximum potential yield. Fruit weight, fruit diameter, number of seeds, and marketable yield were increased in field-grown plants of 'Celebrity', 'Heatwave', and 'Sunny' that were regularly shaken vigorously with an air-blower device, compared to that of plants kept in ambient wind (Hanna, 1999).

For plants grown in still glasshouses it is necessary for growers to use mechanical vibrating devices or imported bees. The mechanical vibrator, also called *vibrating wand* or *electric bee*, when applied to a plant truss can shake pollen free so that it lands on stigmas. However, not all flowers mature at the same time which means that wand treatments must be repeated several times a week. Insects, especially bumble bees, can be cost-effective compared to the labour expense of mechanical pollination; plus, insect pollination is more-or-less continuous rather than intermittent. The use of insect pollinators in glasshouses, however, depends upon pest control practices that protect bees from insecticides. In an unheated glasshouse in Israel, mechanical vibrators and bumble bees had similar effects on fruit set, seed number, fruit size, and yield during autumn and early winter, but the bees were more efficient during cooler winter temperatures than were applications of the vibrator 2–3 times per week (Pressman *et al.*, 1999).

Bumble bees are the most important insect pollinator of tomato, especially in glasshouses. Practical methods for rearing bumble bees year-round were developed in the 1980s (see Chapter 8, page 71), motivated by year-round demand for pollinators of glasshouse tomato. Bumble bees forage normally in glasshouses, and once released in a glasshouse they quickly discover and work tomato flowers. They work flowers when glasshouse temperatures are cool in winter and spring, and they work glasshouse flowers even when the windows are open in summer. The tomato flower is well suited for buzz-pollination, and

Table 49.1. Effectiveness of bumble bees, honey bees, and mechanical vibrators as pollinators of glasshouse tomato 'Cleopatra' in England (Banda and Paxton, 1991).

Pollinator	% fruit-set	Average no. fruit m^{-2}	Average weight (kg) fruit m^{-2}
None	60.1	169	11.3
Honey bees	70.7	198	16.8
Mechanical vibrator	88	202	18.3
Honey bees + vibrator	92.4	205	20.9
Bumble bees	94.9	207	24.3
Bumble bees + vibrator	96.5	208	26.1

Table 49.2. Effectiveness of bumble bees and mechanical vibrators as pollinators of glasshouse tomato 'Dombito' in British Columbia (Dogterom *et al.,* 1998).

Pollinator	Weight (g)	Seed count
None	149 ± 6.8	165.2 ± 8.4
Mechanical vibrator	159.1 ± 7	213.1 ± 11.9
Bumble bees	188.4 ± 4.5	277.8 ± 10.1
Bumble bees + vibrator	181 ± 6	279.5 ± 9.2

bumble bees, unlike honey bees, are capable of buzz-pollinating. Bumble bees are very effective pollinators of glasshouse tomato (Tables 49.1 and 49.2) and the most popular choice of growers. Bumble bee colonies in glasshouses should be fed sugar syrup in order to compensate for the lack of nectar in tomato.

A bumble bee colony has, at most, only a few hundred individuals, and colonies may need to be replaced at intervals during a season. The rearing methods are highly specialized and proprietary. For these reasons, honey bees may retain a role as secondary pollinators of glasshouse tomato, owing to their large colony populations and manageability. In tomato glasshouses, honey bees are disorientated at first but eventually adopt a more organized foraging pattern (Cribb *et al.*, 1993). Honey bees visit relatively few tomato flowers, and because they cannot sonicate the flowers it is difficult for them to collect the pollen. Bee mortality is high, and colonies typically need supplemental sugar syrup and frames of pollen from donor colonies while they are in the glasshouses. In spite of these drawbacks, honey bees compare favourably with mechanical vibrators, at least with varieties 'Criterium' and 'Gold Star' (Table 49.3). The comparative performance of honey bees and vibrators observed by Cribb *et al.* (Table 49.3) differs from that found by Banda and Paxton (Table 49.1). Thus, honey

(a)

(b)

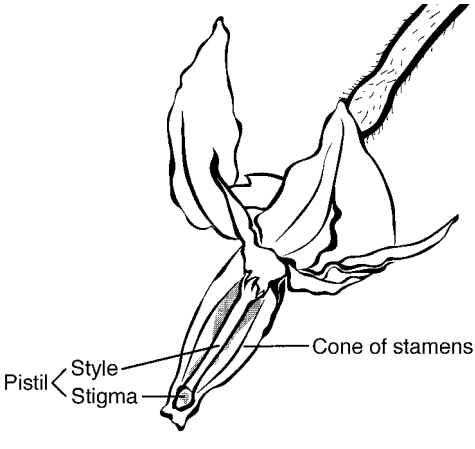


Fig. 49.1. Flower of tomato, *Lycopersicon esculentum*. Flower is shown intact (a) and partially dissected (b) to reveal the pistil surrounded by the cone of stamens. (Source: (art) Darrell Rainey; (photo) Keith S. Delaplane.)

Table 49.3. Effectiveness of honey bees and mechanical vibrators as pollinators of glasshouse tomatoes 'Criterium' and 'Gold Star' in England (Cribb *et al.,* 1993).

Pollinator	% fruit-set	Average no. fruit m^{-2}	Average weight (kg) fruit m^{-2}
	'Criterium'		
None	56	296	22.9
Honey bees	82	431	30.7
Mechanical vibrator	77	391	29.6
Honey bees + vibrator	83	433	30.9
	'Gold Star'		
None	72	326	25.5
Honey bees	88	419	28.5
Mechanical vibrator	81	376	27.5
Honey bees + vibrator	86	411	28.4

bee efficacy on glasshouse tomato may vary across growing conditions and varieties.

There are numerous native bees that pollinate field tomato in the New World tropics, the native range of tomato (Free, 1993). Pollinators can be scarce in other parts of the world (Bohart and Todd, 1961; McGregor, 1976). Although honey bees visit tomato in glasshouses when there is no other choice, they rarely visit tomato in the field. Plant breeders may do well to select for tomato varieties that are more attractive to honey bees and bumble bees. Larger, brighter flowers, functional nectaries, and anthers that allow easier access to pollen would help greatly (Cribb *et al.*, 1993).

There are no recommended bee densities for field tomato. For glasshouses, growers should aim for 4–6 bumble bee colonies $acre^{-1}$ (10–15 ha^{-1}) (van Ravestijn and van der Sande, 1991).

Chapter 50

Watermelon

Flowering

Watermelon (*Citrullus lanatus*) plants are monoecious, bearing both male flowers and female flowers. A few varieties bear perfect flowers and male flowers. Each flower is 1 in (2.5 cm) diameter and pale green or yellow. The petals unite to form a tubular corolla enclosing three stamens that surround a short style and a three-lobed stigma. There are nectaries at the base of the corolla. Flowers open within 2 hours after sunrise. Pollen is usually released before the flower opens, but it stays on the anthers in sticky masses unless it is removed by insects. Stigmas are receptive as long as the flower is open, but receptivity is highest between 9 and 10 a.m. (Adlerz, 1966). Flowers close in the afternoon, never to reopen even if they are not pollinated. Watermelon flowers are attractive to bees for nectar and pollen, but flower density is low and bees are easily distracted away to richer resources.

Watermelon Pollination Requirements

Watermelon is self-fertile, and a female flower is pollinated equally well by pollen from a male flower on the same or different plant. The pollen grains are sticky and insects are required to transfer pollen to receptive stigmas. Fruit abortion in flowers bagged to exclude insects is 100% (Stanghellini *et al.*, 1997). Each stigma needs at least 1000 pollen grains spread evenly over the three lobes in order to form a large, well-shaped fruit (Adlerz, 1966). Fruit will be misshapen and devalued if even one stigma lobe receives an insufficient amount of pollen.

Fruit-set is more likely in ovaries that are longer than $1\frac{1}{8}$ in (28 mm) at the time of pollination compared to ovaries $\frac{3}{4}$ in (20 mm) or smaller (Adlerz, 1966). Plants continue to set fruit throughout a season, but fruit-set is higher in vigorously growing plants. The presence of unhar-

vested cull fruit on a plant inhibits fruit-set of other female flowers; thus, regular harvesting is necessary to optimize fruit-set and yield.

Triploid watermelons are grown for their highly palatable, nearly seedless fruit. Triploid seed is produced by crossing a tetraploid female parent with a selected diploid, or normal, male parent. Tetraploid female parent lines are normally self-sterile, and bees are needed to transfer pollen from the male diploid plants to the tetraploids. Tetraploid (solid colour) rows are alternated with diploid (striped) rows, and seeds are harvested from the tetraploid plants. The plant resulting from triploid seed is sterile, and its small, white seeds are easily eaten along with the fruit (Maynard and Elmstrom, 1992).

Triploid plants, in turn, must be pollinated in order to form fruit. Pollination in this case is not necessary for seed fertilization, but rather for the growth-stimulating effect provided by pollen (Kihara, 1951). Normal diploid varieties can serve as pollenizers. It is most practical to plant the pollenizer in an outside bed, next to two beds of the triploid, followed by another bed of pollenizer, and so forth in a repeating pattern. The diploid pollenizers should be well suited to the same growing regime as the triploid, visually distinguishable from the triploid, and marketable. Early yield of triploids is enhanced when early-blooming icebox watermelons are used as pollenizers, and late yield of triploids is enhanced when standard later-blooming watermelons are used as pollenizers (Maynard, 1990; Maynard and Elmstrom, 1992).

There is genetic variability among watermelon varieties for their attractiveness to bees. Bee visitation was significantly higher in the variety 'BAG' than in 'Sugar Baby' which was associated with nectar of both a higher volume and sugar concentration in 'BAG'. Moreover, this differential attraction to bees was associated with differences in seed set which was higher in 'BAG' (400 seeds per fruit) than in 'Sugar Baby' (225 seeds) (Wolf *et al.*, 1999). This study supports the idea that breeding watermelon varieties for their attraction to bees may help enhance yields.

Watermelon Pollinators

Wind and gravity contribute little or nothing to watermelon pollination. Watermelon is pollinated almost exclusively by insects. Of these, honey bees are the most abundant and widely used (Goff, 1937, 1947). Fruit-set was zero in flowers bagged to exclude bees, but 95% in non-bagged flowers in an Arizona glasshouse stocked with one honey bee colony (Spangler and Moffett, 1979).

Honey bees are reasonably efficient pollinators if they visit watermelon. Flower visitation begins early and peaks between 8 and 10

Table 50.1. Recommended bee densities for watermelon.

No. of honey bee hives acre^{-1} (ha^{-1})	Reference
0.2–5 (0.5–12.4)	McGregor (1976)
2–3 (5–7.4)	Atkins *et al.* (1979)
1 (2.5)	Hughes *et al.* (1982)
1–2 (2.5–5)	Levin (1986)
0.2–2 (0.5–5)	Williams (1994)
1.8 (4.5)	**Literature average**
Other measures	
≥ 8 honey bee visits per flower	Adlerz (1966)
1 honey bee per 100 flowers in all parts of field	Arizona Agricultural Experimental Station and Cooperative Extension Service (1970)

a.m. (Goff, 1937; Adlerz, 1966). Honey bees spend 5.7–8 s per female flower (Adlerz, 1966) which is relatively lengthy and suggests that individual flowers are rich resources. Pollination efficiency may be better if the resources of individual flowers were poorer and bees were forced to visit more flowers. One way to encourage this is to increase competition for flower resources by increasing the density of bee hives in a field. Because each bee spends a long time at a flower, moving very little in the process, it takes at least eight honey bee visits per flower to adequately coat the stigma with pollen and produce a well-shaped fruit (Adlerz, 1966). Seedless triploid varieties produce less pollen than regular diploid watermelon (Ambrose *et al.*, 1995). Thus, triploid varieties probably require more bee visits in order to set fruit; however, this idea is not tested.

Because honey bees are easily distracted away from watermelon, bee attractants may be helpful (see Chapter 7, page 58). However, the record for bee attractants in watermelon is not encouraging. Bee-Scent® increased honey bee visitation in Arizona for up to two days in a seedless variety and in the variety 'Picnic', but it did not increase yield in either variety (Loper and Roselle, 1991). Neither Bee-Scent® nor Beeline® improved bee visitation, yield, or monetary return in 'Royal Sweet' in North Carolina (Schultheis *et al.*, 1994).

Bumble bees are efficient pollinators of watermelon in North Carolina. As the number of bee visits per flower increased, the number of aborted fruit decreased. It took about six honey bee flower visits to reduce fruit abortion to a rate similar to open-pollinated flowers, but bumble bees accomplished this with only one flower visit (Stanghellini *et al.*, 1997). Concerning average seed set per fruit, it took at least 18 honey bee visits per flower, but only 12 bumble bee visits, to achieve a level comparable to that in open-pollinated flowers (Stanghellini *et al.*, 1998).

Chapter 51

Priorities in Technology Development, Research and Education

Never before has the field of bee pollination been better poised for a renaissance in technology development and research, a renaissance propelled by a sense of urgency and an increasing market demand for pollination services. The vulnerable state of pollinators throughout much of the developed world has become a widely recognized phenomenon. It has even captured the attention of the man on the street, thanks to innumerable newspaper articles, television news features, and popular books like S.L. Buchmann and G.P. Nabhan's 1996 *The Forgotten Pollinators*. It is to be hoped that this popular awareness will be translated into higher levels of public and private funding for research and education in crop pollination.

Crop pollination is perhaps the most interdisciplinary field of study in all the agricultural sciences. It requires specialists in botany, entomology, plant breeding, horticulture, agronomy, genetics, bee breeding, ecology, agricultural economics, pheromone biology, and so on. Work in all these specialities is necessary if crop pollination is to mature into a more exact science. For many crops there is still a paucity of information with which one can make good management decisions. All too often the pollination recommendations do not elaborate beyond 'one honey bee hive per acre'. The situation is even worse in the area of bee conservation, a field of study so new to North America that its economic efficacy is yet to be tested.

We hope that this book will serve to synthesize the latest research into useful management recommendations for some of the major pollinator-responsive crops in the temperate developed world. An exercise like this also highlights many gaps in our knowledge. We discuss some of these deficiencies in this chapter in the hope of

highlighting them as research priorities for other workers in the agricultural sciences.

Bee Conservation

Bee conservation for crop pollination enhancement will not develop unless dependable methods for increasing natural bee populations can be demonstrated (Chapter 4). Researchers must develop recommendations for identifying suitable nesting sites, maintaining nesting sites, and protecting bees from natural enemies. Researchers must identify suitable bee pasture plants, preferably on a local basis, and develop recommendations on installing bee plants, managing them, and maintaining bee pastures at optimal stages of plant succession. It is paramount to demonstrate that conservation practices significantly increase local bee populations over the long term.

Bee conservation also will not develop unless conservation practices are shown to be a cost-effective use of agricultural lands. The benefit of lands set aside for bee nesting sites and pasture must be measured as the income realized from increases in yields and fruit quality resulting from improved pollinator populations and pollination. This income must exceed the income possible if those same lands were instead used for conventional production. Closely tied to this is the question of how large the conserved area must be. The bee sanctuary must be 'big enough' to improve pollinator populations significantly when measured against the background of naturally-occurring nest sites and bee plants. Conceivably, a research-derived optimal ratio of tilled lands to conserved lands could be developed on a farm-to-farm, or crop-to-crop, basis.

It is unrealistic to expect growers to divert tillable lands into bee sanctuaries. Thus, an important part of the conservation scheme may be an emphasis on identifying idle acres on a farm – such as fence rows and ditch banks – that can be converted into sanctuaries with little disruption to the grower's cultivation routine. It will require some re-thinking on the part of crop growers who may have little experience or interest in planting and maintaining long-term perennial gardens. We anticipate that conservation programmes will be relatively technology-poor but education-rich.

Managing Non-Honey Bees

Managing and rearing methods for non-honey bee pollinators are poorly developed, with only a few exceptions such as alkali bees and leafcutting bees. Bumble bee rearing is well understood, but only by a

few individuals and companies that guard their methods as proprietary secrets. The relative ease and economy of managing honey bees, *Apis mellifera*, is their greatest advantage over other pollinators. The rearing difficulties of non-honey bees is their greatest liability.

Progress in managing and culturing non-honey bees can be no faster than the basic research on their biology. There are wide gaps in our understanding of the nesting biology, pathology and parasitology, food preferences, reproductive biology, and chemical ecology of many candidate pollinators. Knowledge in these areas could mean the potential to 'seed' habitats with new bee populations, design artificial domiciles, transport nests, propagate bees, attract bees to a crop, and protect bees from predators and parasites. Obstacles, however, have been formidable. Except for the alkali bees (Chapter 9), there are no practical culturing technologies developed for soil-nesting bees.

There remain management problems even for those species that are amenable to culturing. The leafcutting bees are vulnerable to numerous parasites and diseases (Chapter 11), and it is unlikely that orchard bees (Chapter 12) will progress much as pollinators until researchers can develop ways to limit adult dispersal from orchards.

Bombiculture is feasible and even profitable (Chapter 8), but its widespread use in pollination is limited by the high costs of commercially-produced bumble bee colonies. There is still need for research in bumble bee rearing, most especially in the area of inducing cultured queens to produce a second generation. Bumble bee rearing firms all too often rely on repeatedly capturing queens from the wild to start colonies; this raises obvious ecological and ethical questions about harvesting beneficial species from their native habitats for commercial purposes.

It is important to realize that most bee species simply will not prove manageable by man. This may be due to behavioural constraints or to extremely specialized food and nesting requirements. Non-manageability, the inability to be cultured or conserved, is a serious limitation for any candidate pollinator. Their peculiar tolerance towards human management is one of the most distinguishing hallmarks of the honey bee, *A. mellifera*.

Managing Honey Bees

There are serious bee health management problems throughout the honey bee-keeping industries of the world. At the same time, advances in breeding and pheromone biology raise the possibilities of novel management techniques that could improve the utility of honey bees as pollinators. Considering that honey bees are practical and satisfactory pollinators for many crops, these problems and opportunities

justify increasing levels of research funding in order to help sustain this important industry.

The varroa problem

The most pressing problem is the near-worldwide distribution of the parasitic varroa mite (see Chapters 4 and 6). Because of this lethal parasite, honey bees exist now only in managed apiaries in many areas where they once thrived in large wild populations. The loss of large and sustainable feral honey bee populations is a chief cause for the pollination deficit in North America.

Thus, the most immediate research priority for the honey bee industry is varroa mite biology and control. Effective chemical miticides exist and will remain the key to varroa control programmes for the near future. However, there is a growing awareness that the industry must minimize its reliance on chemicals in order to discourage chemical resistance in mites and to preserve the purity of hive products. The well-tested principles of integrated pest management (IPM), the 'integration' of many control methods whether genetic, cultural, biological, or chemical, are now being applied to varroa mites.

Several research teams around the world are studying the mechanisms of genetic mite resistance in bees in the hopes of breeding and propagating resistant bee stocks. Mite-resistant bees would be the most sustainable and cost-effective solution to the mite problem. Progress has been slow as the incidence of varroa resistance in *A. mellifera* is rare. However, there are enough successes to spur hope and justify continued work in this area (Büchler, 1994; Harbo and Hoopingarner, 1997; Spivak and Gilliam, 1998).

Another proven IPM principle is the chemical treatment threshold, defined as the pest density at which a pesticide treatment is warranted in order to prevent the pest from reaching damaging levels. Use of treatment thresholds can eliminate unnecessary chemical applications, but they are most useful when they are worked out on a local basis. So far, varroa treatment thresholds have been identified for Germany (Dietz and Hermann, 1988) and the southeastern US (Delaplane and Hood, 1997), but there is need for similar studies from many more regions of the world.

Pheromone technology and disposable pollination units

Some of the most exciting technology developments in recent years have been with synthetic queen mandibular pheromone (QMP) (see Chapter 7, page 60). QMP-based honey bee attractants have been

tested as pollination aids on apple, blueberry, cherry, cranberry, kiwifruit, and pear, and the field is wide open for testing with many more crops.

Another use for QMP is with disposable pollination units (DPUs) (see Chapter 7, page 61). Queenless, non-reproducing DPUs whose workers are 'stabilized' with QMP could be an attractive pollination option for growers. If the DPUs were made of biodegradable materials, there would be no need for the grower to pick them up at the end of the season. However, DPUs have not been widely adopted, partly because they do not ship well. The availability of synthetic QMP to stabilize queenless workers should revive interest in disposable pollination units, but research is needed in order to develop improved shipping methods.

Controlled matings

Honey bees respond well to selective breeding programmes, and there are many success stories of bees bred to resist diseases and parasites and to preferentially forage for pollen. However, few of these successes have been translated from the laboratory to industry. This is partly because controlled matings are possible only with instrumental insemination or geographically isolated mating 'islands', neither of which is practical for most bee-keepers. The equipment for instrumental insemination and the training to use it are available in North America and Europe (Harbo, 1985), but its cost and microscopic techniques are intimidating to most bee-keepers. Thus, there is need for research in new and simplified methods for making controlled matings. With more practical and inexpensive methods in the hands of bee-keepers, bee breeding could achieve greater importance in bee management and crop pollination.

Crop Pollination Requirements

Our knowledge of the pollination requirements, insect pollinators, and required pollinator densities for most crops is extremely limited. This is the case for many crops represented in this book, namely asparagus, lima bean, snap bean, beet, blackberry, crucifers, carrot, onion, peach and nectarine, pepper, raspberry, soybean, strawberry, and tomato. This kind of research is expensive and difficult because it depends heavily on long hours of human observation. It is also difficult experimentally to partition out the contributions of any one pollinator against the background of normally-occurring pollinators. The existing pollination recommendations for many crops are based

on decades-old research. Age is by no means a drawback to well-executed experiments, but the profound changes in the bee fauna and flora of the developed world in recent years are good cause to dust off our recommendations and subject them to experimental re-examination. It is time for renewed research in the basic pollination requirements for most crops, especially in the identification of relevant pollinators and their required densities.

Plant Breeding

Many of the difficulties in crop pollination derive either from a shortage of pollinators or from the fact that most crop plants are unattractive to bees. Floral attractiveness to bees has historically received little attention from crop breeders. This was not a problem during times when feral honey bee populations were comparatively high, but that is no longer the case in much of the developed world where today most of the agricultural landscapes constitute a 'pollinators' market'. Fewer bees means that individual foragers can better afford to seek out the richest rewards and ignore the rest.

One solution is to increase bee densities and increase competition in order to force bees to visit unattractive crop blooms (see Chapter 7, page 56). The other solution is to make the crop more attractive to bees in the first place. There are several crops represented in this book that are poorly visited by bees but yet require pollination. For example, nectar production is poor in cranberry, onion, pear, pepper, and tomato. The morphology of the tomato flower presents difficulties for bee visitors. Heritability of these traits is not always high (Rabinowitch *et al.*, 1993), but there is a conspicuous shortage of research on the subject. We believe that the pollinator deficit throughout much of the world warrants renewed research and plant breeding initiatives directed at increasing the attractiveness of crop plants to pollinators.

Appendix 1

Bees and Bee-keeping Books and Supplies

Books

A.I. Root Co. (1990) *ABC & XYZ of Bee Culture*, 40th edn. Medina, Ohio.

Bonney, R.E. (1990) *Hive Management: A Seasonal Guide for Bee-keepers*. Garden Way Publishing, Pownal, Vermont.

Buchmann, S.L. and Nabhan, G.P. (1996) *The Forgotten Pollinators*. Island Press/Shearwater Books, Washington DC.

Crane, E. (1990) *Bees and Bee-keeping: Science, Practice and World Resources*. Cornell University Press, Ithaca, New York.

Dafni, A. (1992) *Pollination Ecology: A Practical Approach*. Oxford University Press, New York.

Delaplane, K.S. (1996) *Honey Bees and Bee-keeping: A Year in the Life of an Apiary*, 2nd edn. The Georgia Center for Continuing Education, Athens, Georgia.

Free, J.B. (1993) *Insect Pollination of Crops*, 2nd edn. Academic Press, San Diego.

Frisch, K. von. (1971) *Bees: Their Vision, Chemical Senses, and Language*. Cornell University Press, Ithaca, New York.

Graham, J.M. (ed.) (1992) *The Hive and the Honey Bee*. Dadant & Sons, Hamilton, Illinois.

Griffin, B.L. (1993) *The Orchard Mason Bee*. Knox Cellars Publishing, Bellingham, Washington DC.

Heinrich, B. (1979) *Bumblebee Economics*. Harvard University Press, Cambridge, Massachusetts.

Johansen, C.A. and Mayer, D.F. (1990) *Pollinator Protection: A Bee and Pesticide Handbook*. Wicwas Press, Cheshire, Connecticut.

Maeterlinck, M. (1910) *The Life of the Bee*. Dodd, Mead & Co., New York.

McGregor, S.E. (1976) *Insect Pollination of Cultivated Crop Plants*. US Department of Agriculture, Agriculture Handbook 496.

Michener, C.D. (1974) *The Social Behavior of the Bees: A Comparative Study*. Harvard University Press, Cambridge, Massachusetts.

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Miller, C.C. (1915) *Fifty Years Among the Bees*. A.I. Root Co., Medina, Ohio.

Morse, R.A. (1994) *The New Complete Guide to Beekeeping*. Countryman Press, Woodstock, Vermont.

Morse, R.A. and Hooper, T. (eds) (1985) *The Illustrated Encyclopedia of Bee-keeping*. E.P. Dutton, Inc., New York.

Morse, R.A. and Flottum, K. (eds) (1997) *Honey Bee Pests, Predators, and Diseases*, 3rd edn. A.I. Root Co., Medina, Ohio.

O'Toole, C. and Raw, A. (1991) *Bees of the World*. Blandford, London.

Sammataro, D. and Avitabile, A. (1998) *Bee-keeper's Handbook*, 3rd edn. Cornell University Press, Ithaca, New York.

Seeley, T.D. (1985) *Honeybee Ecology*. Princeton University Press, Princeton, New Jersey.

Sladen, F.W.L. (1912) *The Humble-Bee: Its Life History and How to Domesticate It*. Macmillan, London.

Wilson, E.O. (1971) *The Insect Societies*. Harvard University Press, Cambridge, Massachusetts.

Winston, M.L. (1987) *The Biology of the Honey Bee*. Harvard University Press, Cambridge, Massachusetts.

Honey Bee-keeping Supplies

Australia and New Zealand

Bindaree Bee Supplies, 16 James Street, Curtin ACT 2605, Australia (02) 6281-2111.

Ceracell Beekeeping Supplies, Ltd, 24 Andromeda Crescent, East Tamaki, Auckland, New Zealand (9) 274-7236.

Ecroyd Beekeeping Supplies, Ltd, 26B Sheffield Crescent, Burnside, Christchurch, New Zealand (3) 358-7498.

Redpath's Beekeeping Supplies, 193 Como Parade East, Parkdale, Victoria 3195, Australia (03) 9587-5950.

Europe

E.H. Thorne, Ltd, Wragby, Lincoln LN3 5LA, UK 01673-858555.

Steele and Brodie, 36 College Road, Ringwood, Hampshire BH24 1NX, UK 01425-461734.

Swienty A/S, Hortoftvej 16, DK-6400 Sonderborg, Denmark 74-48-69-69.

Thomas Apiculture, 86 rue Abbé Thomas, F-45450 Fay-aux-Loges, France (0) 2-38-46-88-00.

South Africa

Mountain Bee Products, PO Box 558, Piet Retief 2380, Mpumalanga, South Africa 1782-2768.

USA and Canada

Better Bee Supplies, 265 Avenue Road, Cambridge, Ontario N1R 5S4, Canada, (519) 621-7430.

Brushy Mountain Bee Farm, Inc., Route 1 Box 135, Moravian Falls, North Carolina 28654, USA (800) 233-7929.

Cook's Bee Supplies, Ltd, 91 Edward Street, Aurora, Ontario L4G 1W1, Canada (905) 727-4811.

Dadant & Sons, Inc., Hamilton, Illinois 62341, USA (217) 847-3324.

F.W. Jones & Son, Ltd, 44 Dutch Street, Bedford, Québec L0L 1A0, Canada (514) 248-3323.

Glorybee, 120 N. Seneca Road, Eugene, Oregon 97402, USA (800) 456-7923.

The Bee Works, 5 Edith Drive, Orillia, Ontario L3V 6H2, Canada (705) 326-7171.

The Walter T. Kelley Co., Clarkson, Kentucky 42726, USA (502) 242-2012.

Mann Lake Supply, County Road 40 & First Street, Hackensack, Minnesota 56452, USA (800) 233-6663.

Miller Wood Products, PO Box 2414, White City, Oregon 97503-0414, USA (503) 826-9266.

Rossman Apiaries, Inc., PO Box 905, Moultrie, Georgia 31776, USA (800) 333-7677.

Western Bee Supplies, Inc., PO Box 171, Polson, Montana 59860, USA (406) 883-2918.

Alfalfa Leafcutting Bees and Supplies

Beaver Plastics Ltd, Edmonton, Alberta T5V 1H5, Canada (403) 453-5961.

Cole Wire Products, 2254 Knowles Avenue, Winnipeg, Manitoba R2G 2K6, Canada (204) 452-5886.

Danlo Farms, Box 1210, Beausejor, Manitoba R0E 0C0, Canada (204) 268-3511.

Eggerman Farms Ltd, Box 242, Watson, Saskatchewan S0K 4V0, Canada (306) 287-3780.

Phil Geertson, Route 1 Box 268, Homedale, Idaho 83628, USA (208) 339-3768.

David Getz, Box 66, Birch Hills, Saskatchewan S0J 0G0, Canada (306) 749-2666.

Honeywood Bee Supplies, 309 Timber Drive, Nipawin, Saskatchewan S0E 1E0, Canada (306) 862-5454.

IPS, 1664 Plum Road, Route 4 Box 585, Caldwell, Idaho 83605, USA (208) 454-0086.

IPS, Box 241, Fisher Branch, Manitoba R0C 0Z0, Canada (204) 372-6920.

Bob Kentch Shop, PO Box 582, Touchet, Washington 99360, USA (509) 558-3813.

KLC Bee Farm, Route 4 Box 4077, Wapato, Washington 98951, USA (509) 877-2502.

Mona McPhail, Box 96, Spruce Home, Saskatchewan S0J 2N0, Canada (306) 764-7814.
Mr Pollination Services, Route #8-32-3, Lethbridge, Alberta T1J 4P4, Canada (403) 320-1500.
Muggli LCB Cell Breaking Conveyor, Tounge River Route, Miles City, Montana 59301, USA (406) 232-2058.
Nickel Lane Farms, Box 602, Melville, Saskatchewan S0A 2P0, Canada (306) 728-5549.
Northstar Seed Ltd, PO Box 2220, Neepawa, Manitoba R0J 1H0, Canada (204) 476-5241.
Ray Odermott, Box 863, Nampa, Idaho 83651, USA (208) 465-5280.
Peace River LCB, Box 155, Fairview, Alberta T0H 1L0, Canada (403) 835-4685.
Peterson Leafcutters, Box 97, Parkside, Saskatchewan S0J 2A0, Canada (306) 446-1700.
Prairie Pollinating Ltd, Box 4042, Regina, Saskatchewan, S4P 3R9, Canada (306) 949-3365.
Quality Bee Boards, 15989 Garrity Boulevard, Nampa, Idaho 83687, USA (208) 466-3945.
Ustick Bee Boards, 11133 West Ustick Road, Boise, Idaho 83713, USA (208) 322-7778.
Barry Wolf Farms Ltd, Box 6, Carrot River, Saskatchewan S0E 0L0, Canada (306) 768-3518.
Sheldon Wolf Farms Ltd, Box 761, Carrot River, Saskatchewan S0E 0L0, Canada (306) 768-3257.

Bumble Bee Suppliers

Bees West, Inc., PO Box 1378, Freedom, California 95019, USA (408) 728-3325.
Koppert B.V., Veilingweg 17, PO Box 155, 2650 AD Berkel en Rodenrijs, The Netherlands 10-5140444.
Koppert Biological Systems, Inc., 2856 South Main Street, Ann Arbor, Michigan 48103, USA (313) 998-5589.

Orchard Mason Bee and Bumble Bee-keeping Supplies

Entomo-Logic, 9807 NE 140th Street, Bothell, Washington 98011, USA (206) 820-8037.
Knox Cellars, 1607 Knox Avenue, Bellingham, Washington 98225, USA (360) 733-3283.
Orchard Bee and Supply, 2451 East 3900 South, Salt Lake City, Utah 84124, USA (801) 278-3141.

Cardboard tubes for Orchard Mason bees

Custom Paper Tubes, Inc., 4832 Ridge Road, Cleveland, Ohio 44144, USA (216) 741-0378.

Appendix 2

Sample Bee-keeper/Grower Contract Draft Pollination Agreement For Consideration of Legal Counsel

(modified from Sanford, undated)

This agreement is made _____
(date)

between, _____ , afterwards called grower, and
(grower's name)

_____ , afterwards called bee-keeper.
(bee-keeper's name)

1. TERM OF AGREEMENT
This agreement involves the _____ (year) growing season.

2. RESPONSIBILITIES OF BEE-KEEPER
a. Bee-keeper will supply grower with _____ bee hives delivered to _____ for pollination
(name of orchard or field)

during the applicable growing season as follows: (Fill in appropriate lines and cross out those that do not apply.)

Approximate date: _____

_____ days after written notice from the grower.

Time in relation of amount of crop bloom: _____

_____

Description of hive placement in field: _____

_____

_____

_____

b. Bee-keeper will provide hives of the following minimum standards: A laying queen and:

_____ frames with brood and bees to cover

_____ pounds (kg) of honey stores or other food

_____ -storey hives

Grower may inspect hives after giving reasonable notice to bee-keeper of his intent.

c. Bee-keeper will maintain hives in proper pollinating condition by inspecting, feeding, medicating, or treating for mites as needed.

d. Bee-keeper will leave bees on the crop until: (Fill in appropriate lines and cross out those that do not apply.)

Approximate date: _____

_____days after written notice from the grower.

Time in relation to amount of crop bloom: _____

_____

Other: _____

Bee-keeper will, absent any other notice, remove hives no later than midnight on _____

(date)

e. Bee-keeper is not responsible and, as a condition of this agreement, will be held harmless for inherent risk of bee stings to people, animals, or livestock.

f. Bee-keeper shall/shall not (circle which applies) have the right to harvest bees and/or bee brood from colonies while they are under this contract. In no case shall bee-keeper remove more than 25% of the bees and/or brood.

3. RESPONSIBILITIES OF GROWER

a. Grower will provide a suitable place to locate hives. The site must be accessible to bee-keeper's vehicles. Grower will allow bee-keeper entry whenever necessary to service the bees, and grower assumes full responsibility for all loss and damage to his fields or crops resulting from the use of vehicles over agreed routes in servicing bees.

b. If the grower places bee-keeper's colonies on the crop, grower assumes full responsibility for all loss and damage to colonies resulting from moving colonies to the crop (see section 3d).

c. Grower will not apply highly toxic pesticides to the crop while the bees are being used as pollinators nor immediately before their arrival if residues will endanger the hives. The following agricultural chemicals and methods of application are mutually agreeable while bees are on the crop: _____

_____

_____

_____

_____

_____

_____

_____

Grower will notify bee-keeper 24–48 h in advance if hazardous materials not listed above will be used on the crop being serviced or on adjacent crops. Grower will pay for the cost of moving bees away from and back to the crop to prevent damage from highly toxic materials (see section 3e).

d. Grower will compensate bee-keeper in full for hives destroyed or severely weakened by pesticides or other action by the grower at a rate per hive to be determined by arbitration (see section 5), or, if loss is undisputed, bee-keeper will be compensated by grower at the rate of _____ per hive.

e. Grower will pay for pollination services of _____ hives of bees at the rate of _____ per hive. Payment will be made to the bee-keeper as follows: _____ per hive on delivery and the balance on or before _____
(date)

Additional moves will cost grower _____ per hive per move.

f. Grower will provide adequate sources of water for the bees if none is within $\frac{1}{2}$ mile (0.8 km) of each hive.

g. As a condition of this agreement, grower agrees to hold bee-keeper harmless from any and all claims of injury or damage to person or property which might arise from bee-keeper's performance of this agreement between bee-keeper's placement and removal of hives from grower's fields or orchards.

4. PERFORMANCE

Either party will be excused from obligations of this contract if, before delivery of hives, performance is prevented by events beyond their control. Notification will be given to the other party as soon as reasonably possible.

5. ARBITRATION

If any controversy arises between parties, it will be settled by arbitration. Each party, within 10 days, will appoint one arbitrator, and the two arbitrators will select a third, and the decision of any two arbitrators will be binding on the parties. Cost of arbitration will be divided equally between the two parties.

6. ASSIGNMENT OR TRANSFER

This agreement is not assignable or transferable by either party, except that the terms will be binding on a successor by operation of law.

IN WITNESS WHEREOF, the undersigned parties have made this agreement,

_____

Grower _____

By _____

(address) _____

_____

_____

Bee-keeper _____

By _____

(address) _____

_____

_____

Appendix 3

Table of Pesticides

Toxicity of Pesticides to Honey Bees, Alfalfa Leafcutting Bees and Alkali Bees

The list includes some commonly used insecticides, acaricides, fungicides, plant growth regulators, and herbicides. The use of pesticides is heavily regulated by government agriculture, environmental, and health agencies. It is extremely important to use pesticides only on pests and sites for which they are approved and in a manner consistent with label directions. Some of the pesticides listed below are discontinued by the US Environmental Protection Agency, but are included here as a guide to relative bee toxicity.

Rating Scale:

0 = No data or experience are available. Should not be used in presence of bees.
1 = Should not be applied to blooming plants.
2 = May be applied only in evening after bees have stopped foraging.
3 = May be applied in late evening after bees have stopped foraging until early morning before they begin foraging.
4 = May be applied at any time with reasonable safety to bees.

Pesticide	Honey bee	Alfalfa leafcutting bee	Alkali bee
2,4-D (alkanolamine)	3	0	0
2,4-D (butoxyethanol ester)	3	0	0
2,4-D (isooctyl ester)	4	0	0
2,4-D (isopropyl ester)	3	0	0
2,4-D (sodium salts)	4	0	0
2,4-DB	4	4	4
2,4,5-T	4	0	0
2,4,5-TP	4	0	0
atrazine	4	0	0
Avermectin	2	3	3
azinphos-methyl	1	1	1
Azodrin	1	1	1
Baam	4	0	0
Bacillus thuringiensis[1]	4	4	4
Bactimos	4	4	4
Banvel	4	0	0
Barban	4	0	0
Baycor	4	0	0
Baygon	1	1	1
Baygon G	4	4	4
Baygon ULV	3	0	0
Bayleton	4	0	0
Baytex	1	1	1
Baytex ULV	3	0	0

[1]Not all *Bacillus thuringiensis* insecticides are safe for bees. The label for XenTari® (Abbott Laboratories), with active ingredient *B. thuringiensis aizawai*, reads 'This product is highly toxic to honey bees exposed to direct treatment. Do not apply this product while bees are actively visiting the treatment area'.

Pesticide	Honey bee	Alfalfa leafcutting bee	Alkali bee
Baythroid	1	0	0
Benlate	4	0	0
BHC	1	1	1
Bidrin	1	1	1
Bomyl	1	1	1
Bordeaux Mixture	4	0	0
Brigade	1	1	0
bromacil	3	0	0
Broot G	4	0	0
Butoxone	4	4	4
calcium arsenate	1	1	1
captan	4	0	0
Capture, 0.06 lb or more	1	1	1
Capture, less than 0.06 lb	2	2	0
carboxin	4	0	0
Carbyne	4	0	0
Carzol	3	2	3
Certan	4	4	4
chlordane	3	1	1
Chloro IPC	4	0	0
Cidial	1	1	1
Ciodrin	1	0	0
Comite	4	4	4
Comite + Dylox + Systox	1	1	1
Comply	1	1	1
copper sulphate	4	0	0
cryolite	4	0	0
Cygon	1	1	1
Cymbush	1	1	1
cypermethrin	1	1	1
Cyprex	4	0	0

Pesticide	Honey bee	Alfalfa leafcutting bee	Alkali bee
Cythion	1	1	1
dalapon	4	0	0
Dasanit	1	0	0
DDT	3	1	3
Decis	2	2	2
De-Fend	1	1	1
Delnav	3	2	0
Desiccant (arsenic acid)	4	0	0
Dessin	4	0	0
diazinon	1	1	1
Dibeta	2	2	2
Dibrom	2	2	1
dicofol	4	4	4
dieldrin	1	1	1
Dikar	4	0	0
Dimilin	4	0	0
dinoseb	2	1	1
DiPel	4	4	4
diquat	4	0	0
Disyston EC	3	1	3
Disyston G	4	4	4
Dithane M-22	4	0	0
Dithane M-45	4	0	0
Dithane Z-78	4	0	0
diuron	4	0	0
DNBP	1	1	1
DNOC	3	1	1
Dursban	1	1	1
Dyfonate	3	0	0
Dylox	3	3	3
Elgetol	3	1	1

Pesticide	Honey bee	Alfalfa leafcutting bee	Alkali bee
endothall	3	0	0
endrin	3	1	2
EPN	1	1	1
Eptam	4	0	0
EPTC	4	4	4
ethion	3	1	1
Ethrel	4	0	0
ferbam	4	0	0
Ficam	1	1	1
fixed copper	4	0	0
Florel	4	0	0
flucythrinate	1	0	0
fluvalinate	3	3	2
Folimat	1	0	0
Furadan F	1	1	1
Furadan G	4	4	4
Fury	1	1	1
Fusilade	3	0	0
glyodin	4	0	0
Guthion	1	1	1
Heliothis polyhedrosis virus (Elcar)	4	0	0
heptachlor	1	1	1
Hyvar X	3	0	0
Imidan	1	1	2
IPC	4	0	0
Javelin	4	4	4
Karate	1	1	1
Karathane	4	0	0
Karmex	4	0	0
Kelthane	4	4	4
Kelthane + Dylox + Systox	1	1	1

Pesticide	Honey bee	Alfalfa leafcutting bee	Alkali bee
Kerb	4	0	0
Knox Out	1	1	1
Kryocide	4	0	0
Lance	1	1	1
Lannate	3	2	3
Lannate D	1	1	1
Larvin	3	2	2
Lasso	4	0	0
lead arsenate	1	1	1
Lexone	4	0	0
lime-sulphur	4	4	4
Lindane	1	1	1
Lock-On	1	1	1
Lorsban	1	1	1
MCPA	4	0	0
malathion	2	1	1
Malathion ULV	1	1	1
maneb	4	0	0
Manzeb	4	0	0
Matacil	1	0	0
Mavrik	3	3	2
Measurol	1	1	1
Metacide	1	1	1
Metasystox-R	3	2	3
methoxychlor	3	2	3
methyl parathion	1	1	1
methyl parathion (microencapsulated)	1	1	1
metribuzin	4	0	0
Mitac	4	0	0
Mobilawn	2	0	0

Pesticide	Honey bee	Alfalfa leafcutting bee	Alkali bee
Mocap G	4	0	0
Mocap EC	1	1	1
Monitor	1	1	1
Monobor-Chlorate	4	0	0
Nosema locustae (NoLo Bait)	4	4	4
Nudrin	3	2	3
Nudrin D	1	1	1
oil sprays (Superior type)	3	0	0
Omite	4	4	4
Omite + Dylox + Systox	1	1	1
Orthene	1	1	1
paraquat	4	0	0
parathion	1	1	1
Penncap-M	1	1	1
Pentac	4	0	0
Perthane	3	0	0
Phosdrin	1	1	1
phosphamidon	1	1	1
Phostex	2	0	0
Phygon	4	0	0
picloram	4	0	0
Pirimor	3	3	3
PMA	4	0	0
Pounce	1	1	1
Primicid	1	1	0
Proxol	3	3	2
Pydrin	1	1	1
pyrellin	3	3	3
pyrenone	3	3	3
pyrethrum	4	0	0
Rabon	1	2	3

Pesticide	Honey bee	Alfalfa leafcutting bee	Alkali bee
Rebelate	1	1	1
Resmethrin	1	0	0
rotenone	3	0	0
ryania	3	0	0
Roundup	4	0	0
Savit	2	1	1
Scout	3	2	2
Sencor	4	0	0
Sevimol	1	1	1
Sevin	1	1	1
Sevin 4-Oil	1	1	1
Sevin Bait	4	4	4
Sevin XLR	2	1	1
Sevin XLR Plus	3	1	1
silvex	4	0	0
simazine	3	0	0
Sinbar	4	0	0
Spur	3	2	2
Stalker	2	2	1
Sterling	3	3	3
Stipend	1	1	1
sulphur	4	4	4
Sumithion	1	1	0
Supracide	1	1	1
Systox	3	3	3
Tag	4	0	0
Talstar	1	1	1
Tedion	4	3	4
Teknar	4	4	4
Temik	1	1	1
TEPP	2	1	1

Pesticide	Honey bee	Alfalfa leafcutting bee	Alkali bee
terbacil	4	0	0
Thimet G	3	3	1
Thiodan	3	1	2
thiram	4	0	0
Thuricide	4	4	4
Thylate	4	0	0
Tiovel	3	1	2
Tordon	4	0	0
Treflan	4	4	4
trifluralin	4	4	4
Trithion	3	1	2
Trophy	1	1	1
Vapona	1	1	1
Vendex	4	0	0
Vitavax	4	0	0
Vydate	3	2	2
Zerlate	4	0	0
ziram	4	0	0
Zolone	3	3	3

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